

POLLEN MORPHOLOGY AND RELATIONSHIPS OF THE FLACOURTIACEAE¹

RICHARD C. KEATING²

ABSTRACT

Light microscopic studies of the pollen of 51 genera and 151 species of Flacourtiaceae were made from KOH-acetolyzed specimens. The pollen is always found as single grains and is usually triaperturate with compound apertures, isopolar, and psilate to reticulate. Within the triaperturate type, the pollen of the family ranges from unspecialized to moderately specialized. Differences in pollen morphology do not often serve to delineate the taxonomic tribes. The Berberidopsidae and Oncobae show a considerable range of size and sculpturing patterns. Scolopieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. Pollen of Casariae is similar to that of the preceding group of tribes but adds more specialized trends. Both Pangieae and Paropsieae are isolated in the family, and the Paropsieae should be assigned to the Passifloraceae. Comparisons with families of putatively related orders indicate that the relationships of the Flacourtiaceae based on pollen morphology accord well with Takhtajan's system.

By one recent estimate (Hutchinson, 1967), the Flacourtiaceae include about 90 genera and 1284 species. This large, tropical family has received little attention by taxonomists and morphologists in proportion to its size and evolutionary importance. Such neglect seems to be due to the complex taxonomic history of the family and its reputation as a taxon in which to place many genera of uncertain status (*cf.* Williams, 1965). As understood by Warburg (1893) and Gilg (1925) the family is quite heterogeneous and indeterminate. The concept of the family has been greatly improved by the generic treatment of Hutchinson (1967).

The Flacourtiaceae include some very primitive genera in the tribes Berberidopsidae and Oncobae (Hutchinson, 1967), and the family usually occupies a basal position in the Violales (Cronquist, 1968; Takhtajan, 1969), Cistales (Gundersen, 1950; Thorne, 1968) or Bixales (Hutchinson, 1959). In most of these schemes the Violales are considered close to the Theales, but their relationship to Ranalian lineage is still controversial (Takhtajan, 1969; Meeuse, 1970). A brief resumé of suggested affinities has been presented by Angely (1966). As many as nine orders have been suggested to be derived from flacourtiaceous stock (Takhtajan, 1969), and many of these suggestions will probably prove correct. However, in spite of the potential importance of microscopic characters in interpreting evolutionary trends, such observations are so scarce in many families as to make many statements of taxonomic affinity with Flacourtiaceae fall within the realm of speculation. Recognizing that pollen provides only one line of evidence in phylogenetic studies (Thorne, 1963), I have begun with a survey of the light microscopic features of the pollen in order to provide an

¹ I am grateful to the curators of the U. S. National Herbarium and of the Missouri Botanical Garden for permission to use the collections and for their assistance. The SEM photomicrographs (Figs. 171-172) were made possible through the courtesy of Walter H. Lewis, to whom thanks are extended.

² Department of Biological Sciences, Southern Illinois University, Edwardsville, Illinois 62025.

overview of the family. The value of this feature for comparative investigations has been attested to by many (*cf.* Canright, 1963). More intensive studies of the tribes will include studies of the wall morphology by scanning and transmission electron microscopy of which the present study will provide a basic reference. More detailed studies will definitely be needed to determine the trends of specialization of the wall structure and to better document relationships to other families.

Erdtman (1952, 1969) has called the Flacourtiaceae a eurypalynous family. When considered as understood by Hutchinson (1967) there is diverse pollen morphology, although several of the tribes show a monotonous uniformity. There is less diversity than in the more specialized families of the Malvales and Theales.

In his pollen study of the Alangiaceae, Reitsma (1970*b*) states that the work would not have been possible without reference to the recent monograph of the family. One of the formidable problems in my study was the need to sample herbarium specimens which were not well annotated. Large gaps in the monographic work on the family made the choice of specimens difficult. In order to prevent future confusion, vouchers from each specimen examined are listed by genus.

Previous treatments of flacourtiaceous pollen grains are not common. Erdtman's (1952) study of 25 genera and 35 species included genera which are not presently assigned to the family. Spirlet (1965) and Presting (1965) treated the tribe Paropsieae which has been placed in either the Flacourtiaceae or the Passifloraceae. Rethoré (1963) described pollen of *Tissonia*, *Sabourea*, and *Casearia* of Madagascar. Van Campo *et al.* (1965) and Bronckers (1967) have described pollen of six genera of Flacourtiaceae in their series on African palynology.

MATERIALS AND METHODS

In the present study, 51 genera and 151 species of flacourtiaceous pollen have been examined. Due to their rarity, the three genera included in the tribes Alzateae and Bembicieae are not represented. A number of pollen slides of putatively related genera, especially of Passifloraceae and Tiliaceae, were also prepared or were available for comparison. It has been noted that although the whole ecological amplitude of collections is needed to give a complete picture of pollen morphology, a good picture of a family can also be gained by an extensive rather than an intensive view (Whitehead, 1963).

The material was prepared by KOH-acetolysis (Faegri & Iversen, 1964). This gave clean preparations, and no damage to the exines was observed when compared to acetolysis alone. Expansion is negligible after this treatment (Reitsma, 1969). Pollen was mounted in glycerine-jelly with or without safranin-O added. Several authors have commented on the efficacy of measurements made from treated grains (Dickison, 1967). However, there appears to be no reason why the size and shape of KOH-acetylyzed, glycerine-jelly mounted grains cannot be considered characters in their own right. These methods are widely enough used to preserve the comparative value of such measurements. Whitehead (1965) calculated the conversion factor for pollen mounted in glycerine jelly when compared to silicone oil mounts. Measurements from glycerine-jelly mounts should be divided by 1.06 when compared to silicone-oil preparations.

Measurements of polar (P) and equatorial (E) dimensions were made of at least 20 grains per specimen.

DESCRIPTIONS AND TERMINOLOGY

Descriptive terminology, already overproduced, is further confused by the addition of terminology from electron microscopy. It is important to avoid

confusing appearance with structure. Since most of the recent progress in recognition of wall layers has originated with electron microscopy, one should not use EM inspired terms for optical microscope observations where the structures cannot be clearly seen.

The terminology used here is based on Faegri and Iversen (1964) with some modifications as suggested by Erdtman (1952), Reitsma (1970a), Van Campo (1958), and Wittman and Walker (1965).

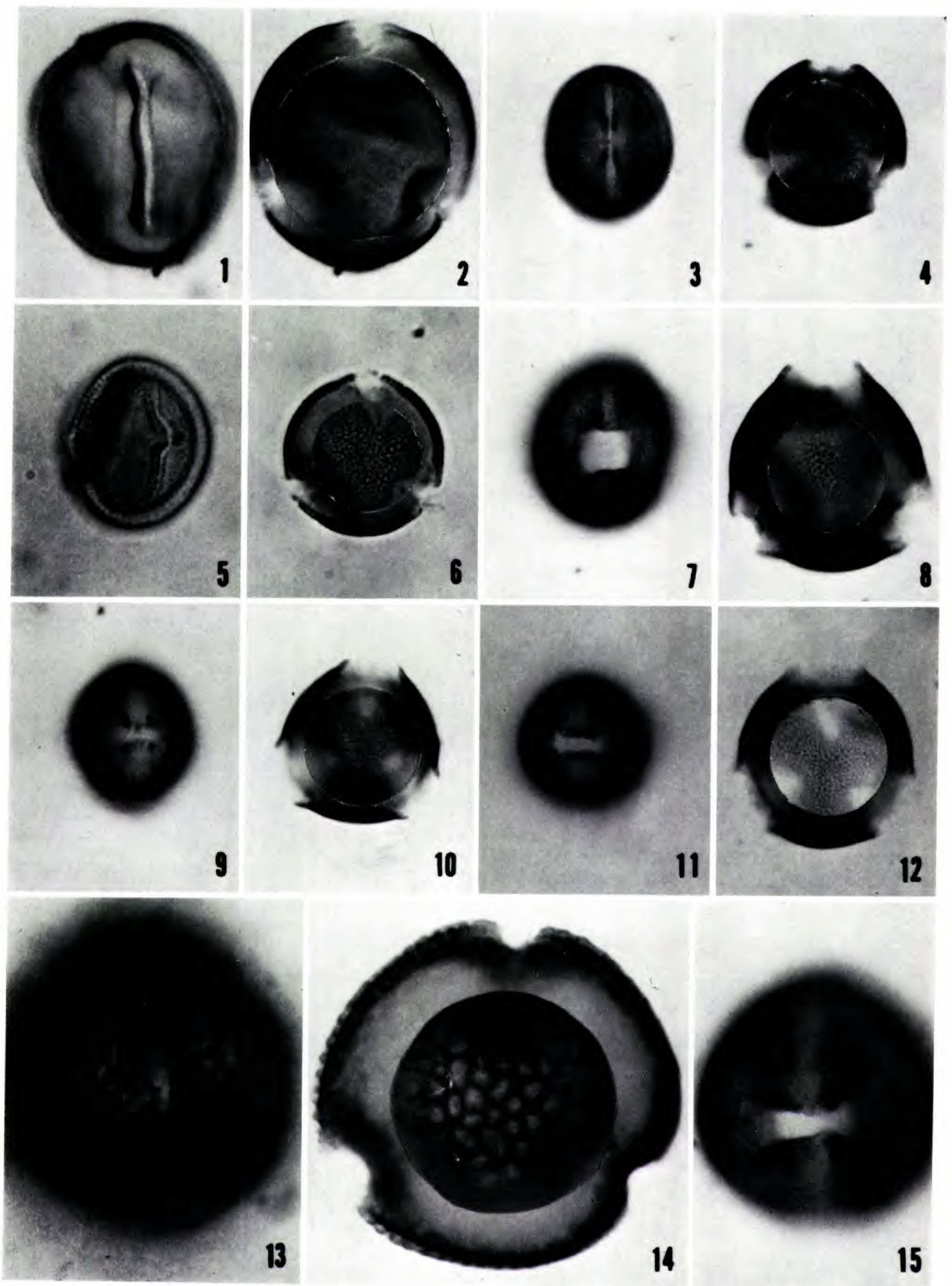
Grains of Flacourtiaceae observed in this study were always single and never in tetrads or larger units. Grains are isopolar in almost all instances. In some cases, *e.g.* *Hecatostemon* (Figs. 171–172), sculpturing elements consistently on one side of the endoaperture produced anisopolar grains, but it was not possible to distinguish the proximal from the distal end.

Shape of the grains is prolate in most genera, but spheroidal grains are also found. Oblate grains are uncommon in the family.

Wall structure and sculpture pattern were occasionally difficult to determine. In optical cross section, most flacourtiaceous grains appeared to have an outer sculptured portion of the exine about equal in thickness to the non-sculptured exine. This observation is not further repeated and, in terms of phylogenetic studies, is not very meaningful. The thickness of the foot layer and other chemically defined layers are not visible with the light microscope. The terms *ektexine* and *endexine* are used when referring to wall layers, since they have been demonstrated to be preferable to other terms (Faegri & Iversen, 1966). Wall thickness usually varies little between the polar and equatorial regions. The total exine thickness in the equatorial region is given in the descriptions.

The patterns of sculpture occasionally caused problems of terminology. Sculpture has been described as “external geometrical features without reference to their internal construction” (Reitsma, 1970a: 46), but in the case of reticulate grains it is difficult to separate the two. Most flacourtiaceous grains have a perforated tectum or reticulate pattern in gradual transitions up to per-reticulate. The smallest muri and lumina are near the limits of resolution at 1000 \times . When these patterns were smaller than 1 μ , L-O patterns were often helpful in determining the structure. The terms *simpli-* or *duplibaculate* are used to describe muri supported by single or double rows of baculae (*Columellae*), when either condition is visible.

Apertures in the Flacourtiaceae are always meridionally and zonally arranged, the edges being more or less level with the exine. The apertures are almost always compound, consisting of a wide or narrow colpus (*ectoaperture*) which is lens shaped with pointed ends converging on the polar areas. A distinct aperture-free polar area is always present at both ends. Edges of the colpi are distinct and straight unless noted as being ragged or obscure. An inner aperture (*endoaperture*, Van Campo, 1958) is usually present and found in the *endexine* (Figs. 171–172). The equatorially placed *endoaperture* is usually equatorially elongate beyond the edges of the colpus, often with truncate or indeterminate ends. Distinctness of these apertures is noted in the descriptions and is highly variable. This kind of aperture has been called a “*colpus transversales*” (Faegri & Iversen, 1964), if it has a length-breadth ratio of greater than 2 (Reitsma, 1970b). *Endo-*



FIGURES 1-15. Pollen of Flacourtiaceae, tribes Berberidopsidae and Oncobaeae, $\times 1000$.—1-12. Berberidopsidae.—1-2. *Berberidopsis corallina* (Philippi s. n.).—1. Equatorial view of colpus.—2. Polar view, optical cross section and polar surface.—3-4. *Erythrospermum acuminatissimum* (Smith 1254).—3. Equatorial view of colpus.—4. Polar view, optical cross section and finely reticulate polar surface.—5-6. *Ahernia glandulosa* (Loher 5568).—5. Equatorial view of colpus.—6. Polar view, optical cross section and finely reticulate polar surface.—7-8. *Dasylepis leretii* (DeGiorgi 1738).—7. Equatorial view of colpus and pore.—8. Polar

apertures with less than this ratio have been called porae or ora. It has been stated that "a porus is supposed to be nothing more than a short colpus" (Reitsma, 1970b: 284), but it has not been demonstrated that the elongate endoaperture described here is homologous with all other types of pores occupying the centers of colpi. Therefore, I will retain the more purely descriptive term "endoaperture" which at least accurately reflects placement in the endexine layer.

Thickenings in the endexine layer bordering the apertures, the costae, occur in most species observed. Costae may outline only the ectoaperture, the endoaperture, both, or may be restricted to the four corners of the intersection of the two apertures. The colpi "membranes" are usually free of sculpturing elements.

A number of genera have colpi with endoapertures being either obscure or absent. Grains are called colporoidate, if the equatorial area of the colpus has lighter optical density or shows a constriction.

The distribution of grain sizes is mostly limited to Erdtman's (1952) categories of small (10-25 μ) and medium-sized (25-50 μ).

OBSERVATIONS

BERBERIDOPSISIDAE

Berberidopsis Hook. f. Figs. 1-2.

Pollen grains spheroidal to prolate spheroidal. Structure obscure but probably tectate, no baculae seen. Psilate. Exine thickness 1.5 μ . Tricolpate, colpi delimitation distinct, not costate. Average size: P = 25-30 μ ; E = 30-33 μ .

Specimen examined: *B. corallina* J. D. Hook.—Chile, *Philippi s. n.* (US).

Erythrospermum Lam. Figs. 3-4.

Pollen grains prolate-spheroidal. Structure obscure but probably tectate. Finely verrucate. Exine thickness 1.5 μ . Tricolpate-tricolporoidate. Colpi may be constricted at equator. Faintly costate. Average size: P = 19 μ ; E = 18 μ .

Specimen examined: *E. acuminatissimum* (A. Gray) A. C. Sm.—Fiji, *Smith 1254* (US).

Ahernia Merrill Figs. 5-6.

Pollen grains spheroidal to prolate-spheroidal, semitectate, reticulate, lumen less than 1 μ . Exine thickness 1.5 μ . Tricolporoidate. Colpi constricted at the equator. Faintly costate. Average size: P = 18-20 μ ; E = 18 μ .

Specimen examined: *A. glandulosa* Merr.—Philippines, *Loher 5568* (US).

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view, optical cross section and finely reticulate polar surface.—9-10. *Scottellia klaineana* (Klaine 3438).—9. Equatorial view of pore.—10. Polar view, optical cross section and finely reticulate polar surface.—11-12. *S. coriacea* (Kennedy 1674).—11. Equatorial view of pore.—12. Polar view, optical cross section and finely reticulate polar surface.—13-15. Oncobaeae. 13-14. *Carpotroche platyptera* (Kuylen 69x).—13. Equatorial view of colpus.—14. Polar view, optical cross section and coarsely reticulate surface.—15. *C. sp.* (*Froes 21101*). Equatorial view, internal surface of pore.

Dasylepis Oliv. Figs. 7–8.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen $0.3\text{--}0.5\mu$. Exine thickness $1.5\text{--}2\mu$. Tricolporate, endoapertures rectangular, equatorially elongate. Colpi costate. Average size: $P = 25\mu$; $E = 23\text{--}25\mu$.

Specimens examined: *D. lereti* DeWild.—West Africa, *De Giorgi 1738* (US). *D. integra* Warb.—West Africa, *Holst 1220* (US).

Scottellia Oliv. Figs. 9–12.

Pollen grains spheroidal, semitectate, reticulate. Baculae not visible, lumen less than 1μ . Exine thickness 1.5μ . Tricolporate, endoapertures rectangular, costate, equatorially elongate. Average size: $P = 18\text{--}20\mu$; $E = 18\text{--}20\mu$.

Specimens examined: *S. coriacea* A. Chev.—Nigeria, *Kennedy 1674* (US). *S. klaineana* Poire—Gabon, *Klaine 3438* (US).

ONCOBEAE

Carpotroche Endl. Figs. 13–15.

Pollen grains spheroidal, semitectate, finely reticulate to duplibaculate and per-reticulate, lumen $0.1\text{--}4\mu$. Exine thickness $1.5\text{--}4\mu$. Tricolpor(-oid-)ate, endoapertures may be costate but faintly delimited. Average size: $P = 37\text{--}40\mu$; $E = 37\text{--}40\mu$.

Specimens examined: *C. platyptera* Pittier—Honduras, *Kuylen 69x* (US). *C. sp.*—Brazil, *Fróes 21101* (US).

Mayna Aubl. Figs. 16–19.

Pollen grains spheroidal, semitectate, reticulate or per-reticulate, simpli- or duplibaculate. Lumen $1\text{--}4.5\mu$. Exine thickness $1.5\text{--}2.5\mu$. Tricolpor(-oid-)ate. Colpi costate near endoapertures, delimitation of endoapertures diffuse. Average size: $P = 33\text{--}50\mu$; $E = 33\text{--}46\mu$.

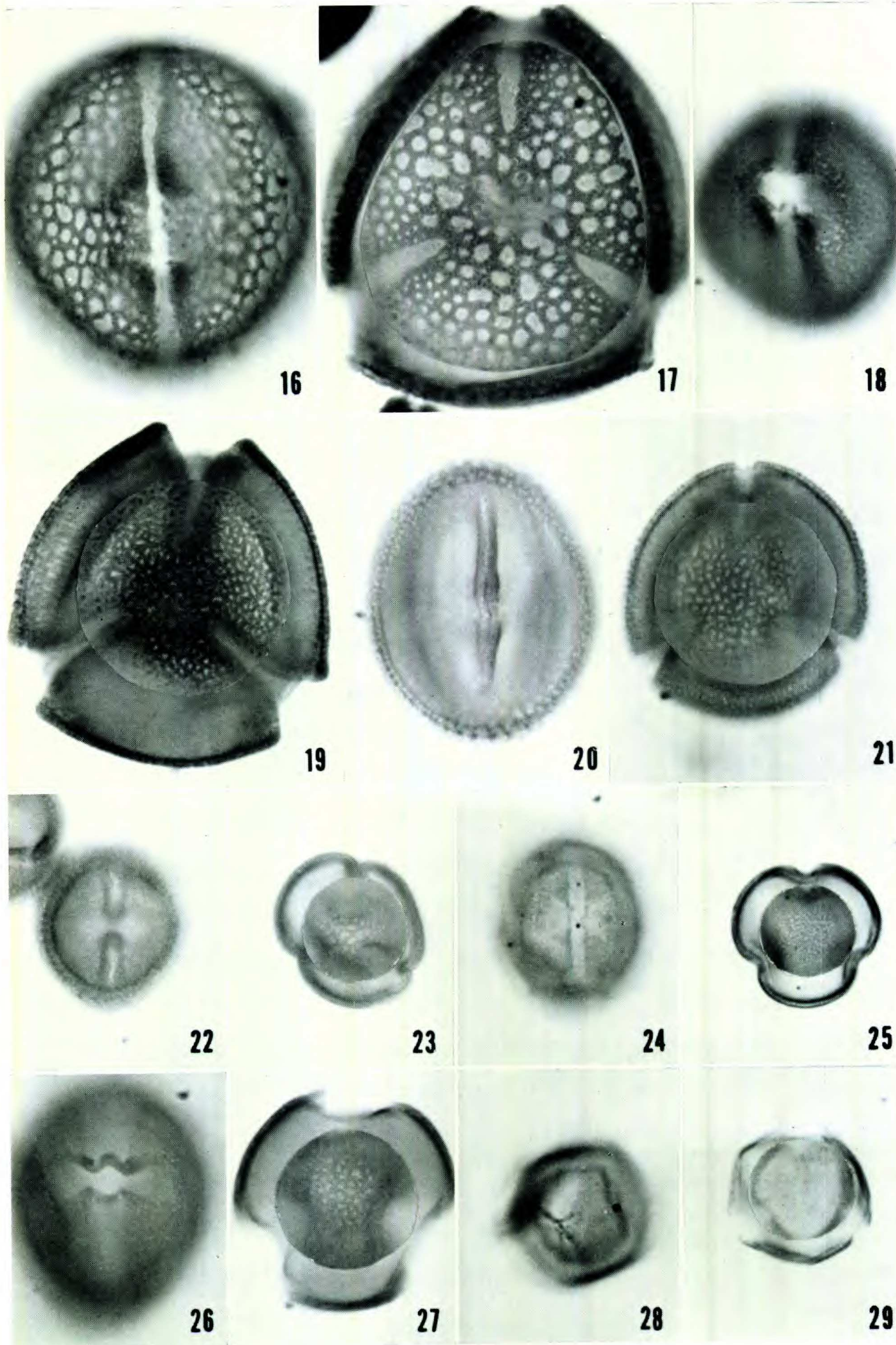
Specimens examined: *M. echinata* Spruce—Peru, *Klug 3808* (US). *M. longifolia* P. & E. var *heliocarpa* R. E. Schult.—Brazil, *Schultes 6593* (US). *M. odorata* Aubl.—Brazil, *Ducke 15156* (US).

Oncoba Forsk. Figs. 20–21.

Pollen grains prolate-spheroidal, semitectate, reticulate to per-reticulate, simplibaculate. Lumen $0.5\text{--}1.5\mu$. Exine thickness $1\text{--}2\mu$. Tricolporoidate, costate, endoaperture delimitation diffuse. Average size: $P = 20\text{--}30\mu$; $E = 20\text{--}30\mu$.

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FIGURES 16–29. Pollen of Flacourtiaceae, tribe Oncobae, $\times 1000$.—16–17. *Mayna longifolia* (*Schultes 6593*).—16. Equatorial view showing colpus and pore.—17. Polar view, optical cross section and coarsely reticulate, duplibacculate polar surface.—18–19. *M. odorata* (*Ducke 15156*).—18. Equatorial view of pore.—19. Polar view, optical cross section and reticulate polar surface.—20–21. *Oncoba spinosa* (*Jack 6549*).—20. Equatorial view of colpus.—21. Polar view, optical cross section and reticulate polar surface.—22–23. *Caloncoba echinata* (*Jack 4744*).—22. Equatorial view of colpus divided by an equatorial bridge.—23. Polar view, optical cross section and reticulate polar surface.—24–25. *Lindackeria dentata* (*Lebrun 6780*).—24. Equatorial view of colpus.—25. Polar view, optical cross section and finely reticulate polar surface.—26–27. *Poggea kameruunensis* (*Zenker 239*).—26. Equatorial view, internal surface at pore.—27. Polar view, optical cross section and reticulate polar surface.—28–29. *Buchnerodendron speciosum* (*Robyns 1336*).—28. Equatorial view.—29. Polar view, optical cross section and polar surface.



Specimens examined: *O. laurina* (Presl) Warb.—Panama, *Allen 3665* (US). *O. spinosa* Forsk.—Cuba, *Jack 6549* (US).

Caloncoba Gilg Figs. 22–23.

Pollen grains prolate-spheroidal, tectate, reticulate to finely reticulate, simplibaculate, lumen $0.1\text{--}0.5\mu$. Exine thickness $1\text{--}2\mu$. Tricolporoidate, colpi divided transversely by a bridge in the ectexine. Average size: $P = 20\text{--}38\mu$; $E = 23\text{--}35\mu$.

Specimens examined: *C. brevipes* Gilg—Ghana, *Fairchild 1223* (US). *C. echinata* (Oliv.) Gilg—Cuba, *Jack 4744* (US). *C. glauca* (Oliv.) Gilg—Congo, *Robyns 1194* (US).

Lindackeria Presl Figs. 24–25.

Pollen grains prolate-spheroidal to prolate, semitectate or tectate, reticulate to finely reticulate, lumen $0.2\text{--}1\mu$. Exine thickness $1.5\text{--}2\mu$. Tricolporoidate, costate in some specimens, delimitation of endoapertures may be diffuse. Average size: $P = 18\text{--}30\mu$; $E = 18\text{--}30\mu$.

Specimens examined: *L. dentata* (Oliv.) Gilg—Central Africa, *Troupin 6362* (US). Congo, *Lebrun 6780* (US). *L. paludosa* (Benth.) Gilg—Venezuela, *Holt & Blake 693* (US). *L. Poggei* (Gürke) Gilg—Congo, *Gossweiler 8664* (US).

Poggea Gürke Figs. 26–27.

Pollen grains prolate-spheroidal. Structure tectate, reticulate, simplibaculate. Lumen $0.7\text{--}1\mu$. Exine thickness 1.5μ . Tricolporate, occasionally tetracolporate, endoaperture equatorially elongate with transverse costae. Endoaperture delimitation diffuse at ends. Average size: $P = 28\text{--}30\mu$; $E = 25\text{--}28\mu$.

Specimen examined: *P. kameruunensis* Gilg—Cameroons, *Zenker 239* (US).

Buchnerodendron Gürke Figs. 28–29.

Pollen grains spheroidal, tectate, finely reticulate, lumen $0.2\text{--}0.5\mu$. Exine thickness 1μ . Tricolpate, tricolporoidate. Apertures diffuse and difficult to orient. Average size: $P = 18\text{--}20\mu$; $E = 18\text{--}20\mu$.

Specimen examined: *B. speciosum* Gürke—Congo, *Robyns 1336* (US).

SCOLOPIEAE

Scolopia Schreb. Figs. 30–34.

Pollen grains prolate spheroidal to prolate, tectate, reticulate, lumen $0.3\text{--}1\mu$. Exine thickness $1\text{--}2\mu$. Tricolporoidate, colpi costate, endoapertures diffuse at edges. Average size: $P = 23\text{--}25\mu$; $E = 18\text{--}23\mu$.

Specimens examined: *S. brownii* F. v. M.—Australia, *Leonhardt s. n.* (US). *S. cochinchinensis* (Lour.) Clos—Viet Nam, *Clemans 3833* (US). *S. eckloni* Szysz.—South Africa, *Wood s. n.* (US). *S. luzonensis* Warb.—Philippines, *Elmer 5625* (US). *S. oldhamii* Hance—Formosa, *Wilson 10781* (US).

BANAREAE

Banara Aubl. Figs. 35–37.

Pollen grains prolate-spheroidal, tectate, reticulate. Lumen $0.5\text{--}1\mu$. Exine thickness 1μ . tricolpor(-oid-)ate, costate, endoapertures diffuse, equatorially

elongate. Average size: $P = 15-28\mu$; $E = 13-23\mu$.—This description does not apply to *B. costaricensis* Figs. 44-45.

Specimens examined: *B. guinensis* Aubl.—Venezuela, *Pittier 11606* (US). *B. mollis* Tul.—Peru, *Klug 3301* (US). *B. costaricensis* (Standl.) Sleumer.—Costa Rica, *Holm & Iltis 787* (US).

Pineda Ruiz & Pav. Figs. 40-41.

Pollen grains prolate-spheroidal, tectate, simplibaculate, reticulate; lumen 0.5μ . Exine thickness 2μ . Tricolporoidate, colpi costate; equatorial bridge in the ektexine may replace diffuse endoaperture. Average size: $P = 23-25\mu$; $E = 18-20\mu$.

Specimen examined: *P. incana* R. & P.—Peru, *Vargas 7596* (US).

Trimeria Harv. Figs. 42-43.

Pollen grains prolate, tectate, reticulate. Lumen $1-1.5\mu$. Exine thickness $1.3-2\mu$. Tricolporate to tricolporoidate, costate, endoapertures equatorially elongate or replaced by an equatorial bridge in the ektexine. Average size: $P = 18-20\mu$; $E = 13-15\mu$.

Specimen examined: *T. alnifolia* Planch.—Praetoria, *Ratray 313* (US).

Pleuranthodendron L. O. Wms. Figs. 38-39.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen $0.5-1\mu$. Exine thickness 1μ . Tricolpor(-oid-)ate, costate, endoapertures diffuse. Average size: $P = 15-18\mu$; $E = 13-15\mu$.

Specimen examined: *P. mexicana* (A. Gray) L. O. Wms.—Mexico, *Mexia 9284* (US).

HOMALIEAE

Dissomeria Benth. Figs. 46-47.

Pollen grains prolate, tectate, reticulate, lumen 0.3μ . Exine thickness 2μ . Apertures tricolporate, costate, endoapertures equatorially elongate. Average size: $P = 25-30\mu$; $E = 20-25\mu$.

Specimen examined: *D. crenata* Benth.—Ghana, *Vique 1550* (US).

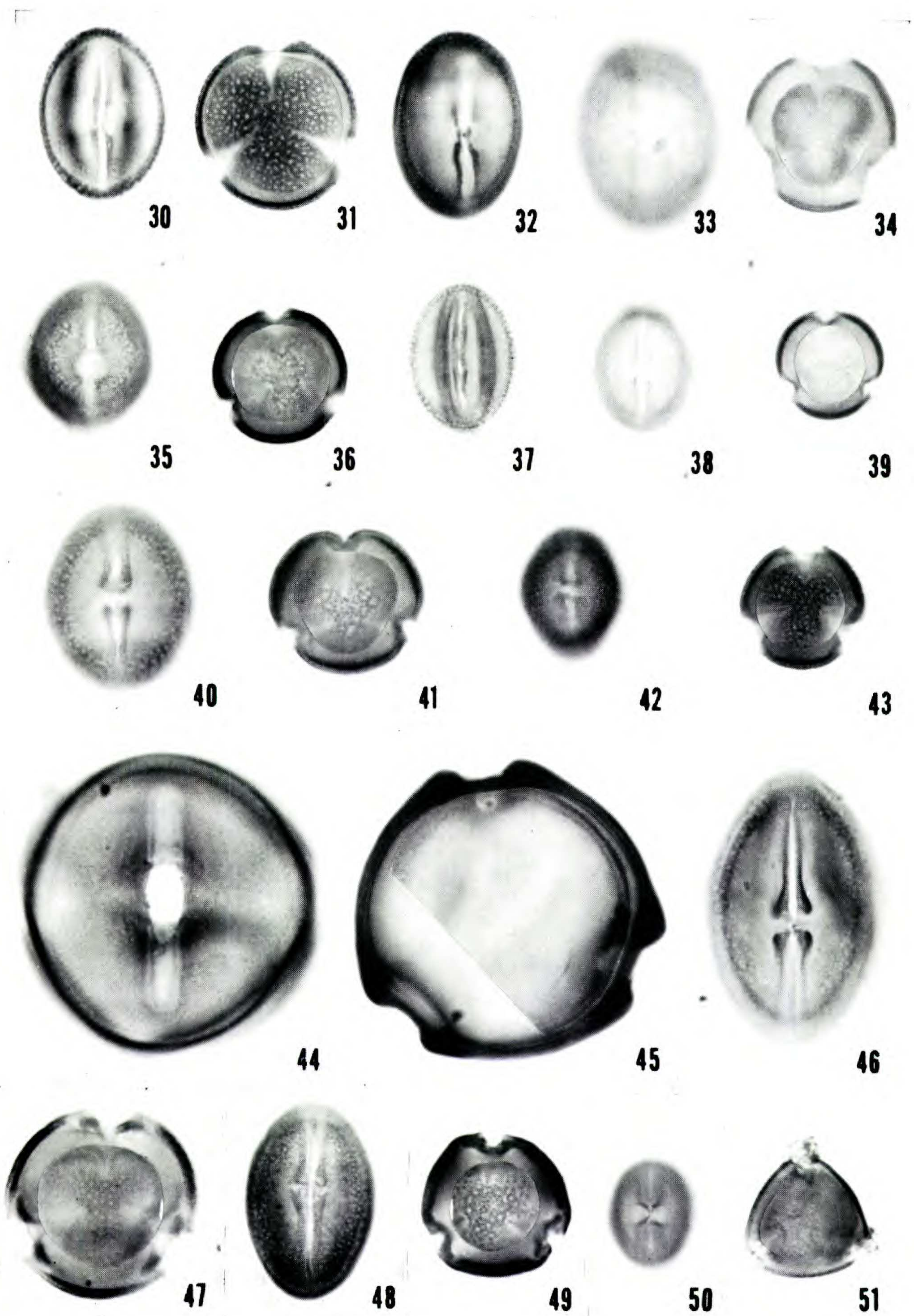
Calantica Jaub. ex. Tul. Figs. 48-49.

Pollen grains prolate, tectate, finely reticulate, lumen $0.7-1\mu$. Exine thickness 2μ . Tricolporate, costate, endoapertures equatorially elongate, edges diffuse. Average size: $P = 28-30\mu$; $E = 20-23\mu$.

Specimen examined: *C. ceratifolia* Endl.—Madagascar, *Hildebrandt 3817* (US).

Homalium Jacq. Figs. 52-59.

Pollen grains prolate, tectate, finely reticulate to obscure, lumen $0.3-1\mu$. Exine thickness $1.5-2\mu$. Tricolporate, costate, endoapertures equatorially elongate with constricted, or branched, indeterminate ends. Occasional ektexine elements on the colpi membrane above or below endoapertures. Average size: $P = 15-35\mu$; $E = 13-25\mu$.



Specimens examined: *H. bracteatum* Benth.—Philippines, *Darling 18691* (US). *H. cochinchinensis* (Lour.) Druce—Hong Kong, *Taam 2015* (US). *H. deplanchei* Warb.—New Caledonia, *McKee 7963* (US). *H. guianense* (Aubl.) Warb.—British Guiana, *Smith 2664* (US). *H. hainanense* Gagnep.—China, *Lei 399* (US). *H. hosei* Merr.—Borneo, *Ramos 1174* (US). *H. humblotii* H. Bn.—Madagascar, *Humblot 582* (US). *H. involucratum* (DC.) H. Bn.—Madagascar, *Hildebrandt 3310* (US). *H. nepaulense* (DC.) Benth.—Nepal, *Nicolson 2504* (US). *H. racemosum* Jacq.—Panama, *Pittier 2693* (US). *H. stenophyllum* Merr. & Chun—China, *Chun & Tso 43732* (US). *H. stipulaceum* Welw.—Congo, *Gossweiler 8525* (US). *H. tomentosum* (Vent.) Benth.—Burma, *Mikee 5969* (US).

Gerrardina Oliv. Figs. 50–51.

Pollen grains spheroidal, subangulaperturate, tectate, finely reticulate, lumen 0.5–1.2 μ . Exine thickness 1 μ . Tricolpor-(oid-)ate, costate, endoapertures diffuse, equatorially elongate. Average size: P = 13–15 μ ; E = 13–15 μ .

Specimens examined: *G. eylesiana* Milne-Redh.—Nyasaland, *Brass 16641* (US).

PANGIEAE

Hydnocarpus Gaertn. Figs. 62–63.

Pollen grains spheroidal, semitectate, per-reticulate, simplibaculate, lumen 2–6 μ . Exine thickness 4.5 μ . Tricolporate, costae not visible, endoapertures probably equatorially elongate but obscured by heavy reticulum. Average size: P = 33–43 μ ; E = 33–35 μ .

Specimens examined: *H. calophylla* (Ridl.) Sleum.—Borneo, *Jacobs 5181* (US). *H. ilicifolia* King—Viet Nam, *Petelot s. n.* (US). *H. wightiana* Blume—Brazil, *Krug 4315* (US).

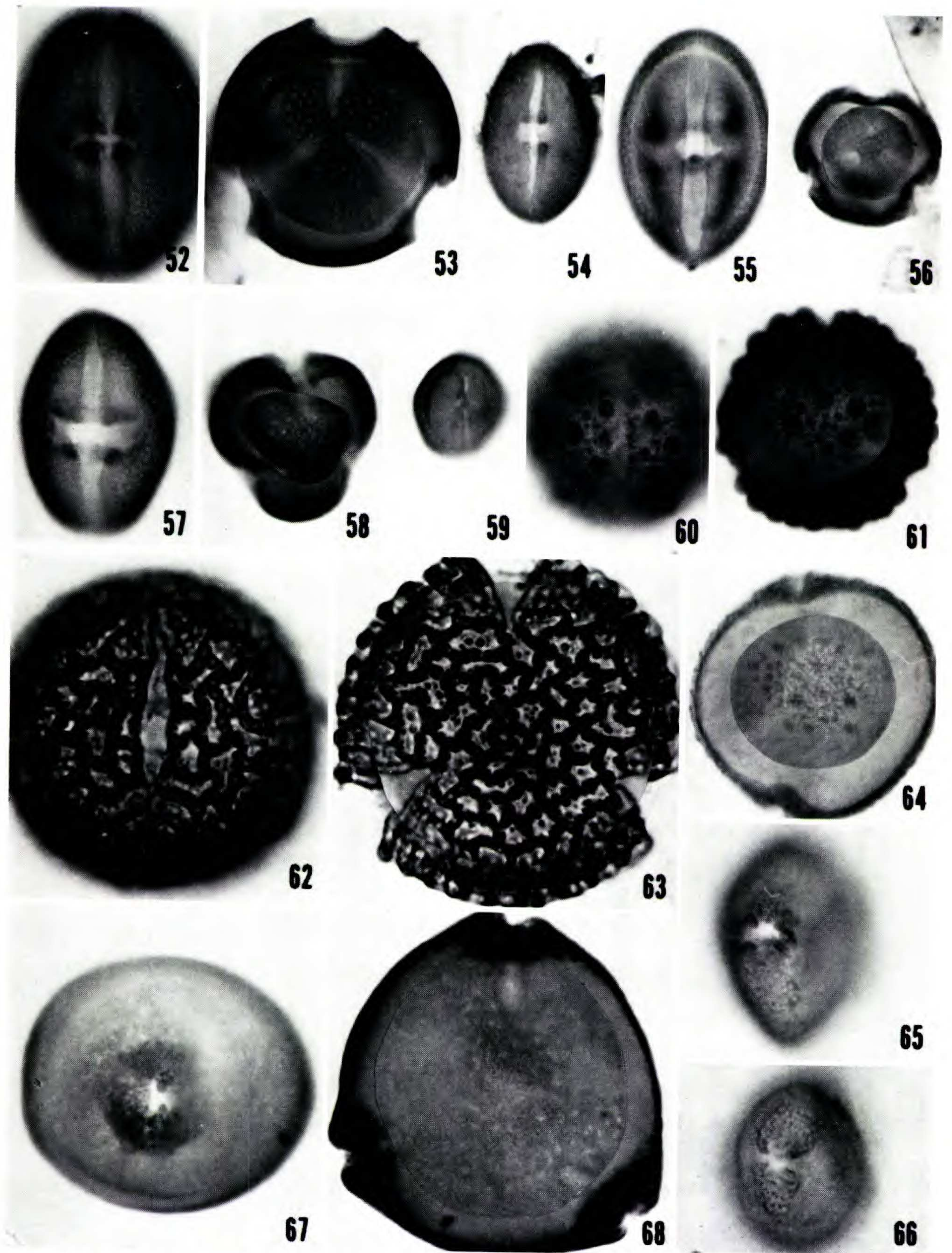
Pangium Reinw. Figs. 67–68.

Pollen grains oblate-spheroidal. Exine with perforated tectum with uniformly closely spaced baculae visible. No measurable lumen. Exine thickness 1.5–2 μ . Tricolporate, endoapertures equatorially elongate with margins having baculate proliferations. Colpi obscure. Average size: P = 33–38 μ ; E = 40–45 μ .

Specimen examined: *P. edule* Reinw.—New Guinea, *Brass 27673* (US).

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FIGURES 30–51. Pollen of Flacourtiaceae, tribes Scolopieae, Banareae, and Homalieae, $\times 1000$.—30–34. Scolopieae.—30–31. *Scolopia cochinchinensis* (*Clemens 3833*).—30. Equatorial view of colpus.—31. Polar view, optical cross section and reticulate polar surface.—32. *S. brownii* (*Leonhardt s. n.*), equatorial view of colpus.—33–34. *S. luzonensis* (*Elmer 5625*).—33. Equatorial view.—34. Polar view, optical cross section and polar surface.—35–45. Banareae.—35–36. *Banara guinensis* (*Pittier 11606*).—35. Equatorial view of colpus and pore.—36. Polar view, optical cross section and finely reticulate polar surface.—37. *B. mollis* (*Klug 3301*), equatorial view of colpus.—38–39. *Pleuranthodendron mexicana* (*Mexia 9284*).—38. Equatorial view of colpus.—39. Polar view, optical cross section and finely reticulate polar surface.—40–41. *Pineda incana* (*Vargas 7596*).—40. Equatorial view of colpus.—41. Polar view, optical cross section and reticulate polar surface.—42–43. *Trimeria alnifolia* (*Ratray 313*).—42. Equatorial view showing colpus.—43. Polar view, optical cross section and finely reticulate polar surface.—44–45. *Banara costaricensis* (*Holm & Iltis 787*).—44. Equatorial view of colpus and pore.—45. Polar view, optical cross section and polar surface.—46–51. Homalieae.—46–47. *Dissomeria crenata* (*Vique 1550*).—46. Equatorial view of colpus and costae.—47. Polar view, optical cross section and finely reticulate polar surface.—48–49. *Calantica ceratifolia* (*Hildebrandt 3817*).—48. Equatorial view of colpus.—49. Polar view, optical cross section and finely reticulate polar surface.—50–51. *Gerrardina eylesiana* (*Brass 16641*).—50. Equatorial view with colpus.—51. Polar view, optical cross section and polar surface.



FIGURES 52-68.—Pollen of Flacourtiaceae, tribes Homalieae and Pangieae, $\times 1000$.—52-59. Homalieae.—52-53. *Homalium racemosum* (Pittier 2693).—52. Equatorial view with colpus and pore.—53. Polar view, optical cross section and reticulate polar surface.—54. *H. humblotii* (Humblot 582), equatorial view with colpus and pore.—55-56. *H. bracteatum* (Darling 18691).—55. Equatorial view with colpus and pore.—56. Polar view, optical cross section and finely reticulate polar surface.—57-58. *H. guianense* (Smith 2664).—57. Equatorial view with colpus and pore.—58. Polar view, optical cross section and finely reticulate polar surface.—59. *H. hainanensis* (Lei 399), equatorial view.—60-68. Pangieae.—60-61. *Trichadenia philippinensis* (Ahern 2982).—60. Equatorial view with colpus.—61. Polar view,

Trichadenia Thw. Figs. 60–61.

Pollen oblate-spheroidal, intectate, baculate and verrucate in a mixed, random pattern. Bacules to 3μ high, verrucae to 4μ wide and high. Exine thickness $5\text{--}6\mu$. Tricolporate, costate, endoapertures distinct and variable. Colpi diffuse. Average size: $P = 33\text{--}38\mu$; $E = 40\text{--}45\mu$.

Specimen examined: *T. philippensis* Merr.—Philippines, *Ahern* 2982 (US).

Ryparosa Bl. Figs. 64–66.

Pollen grains prolate-spheroidal, tectate, finely reticulate, lumen $0.2\text{--}0.5\mu$. Exine thickness $1.5\text{--}2\mu$. Tri (bi-)colpate or tricolporate, endoapertures distinct, the margins with small processes extending over the opening. Colpi diffuse. Average size: $P = 20\text{--}27\mu$; $E = 18\text{--}23\mu$.

Specimens examined: *R. acuminata* Merr.—Borneo, *Ramos* 1367 (US). *R. hirsuta* J. J. Sm.—Borneo, *Agama* 662 (US). *R. wrayi* King—Sumatra, *Bartlett* 8410 (US).

Kiggelaria L. Figs. 69–71.

Pollen grains prolate to prolate-spheroidal, tectate with a finely granular pattern. Exine thickness $2\text{--}2.5\mu$. Tricolpor(-oid-)ate, endoapertures constricted or equatorially elongate. Costae prominent. Average size: $P = 30\text{--}45\mu$; $E = 33 = 45\mu$.

Specimens examined: *K. africana* L.—Transvaal, *Schlieben* 7341 (US). *K. integrifolia* Jacq.—South Africa, *Ecklon & Zeyler s. n.* (US).

FLACOURTIACEAE

Bennettiodendron Merrill Figs. 72–73.

Pollen grains subprolate, semitectate, reticulate, lumen $0.5\text{--}1.5\mu$. Exine thickness 1.5μ . Tricolpor(-oid-)ate, weakly costate, endoapertures equatorially elongate with diffuse ends. Ends of colpi occasionally connect over poles. Average size: $P = 18\text{--}20\mu$; $E = 18\text{--}20\mu$.

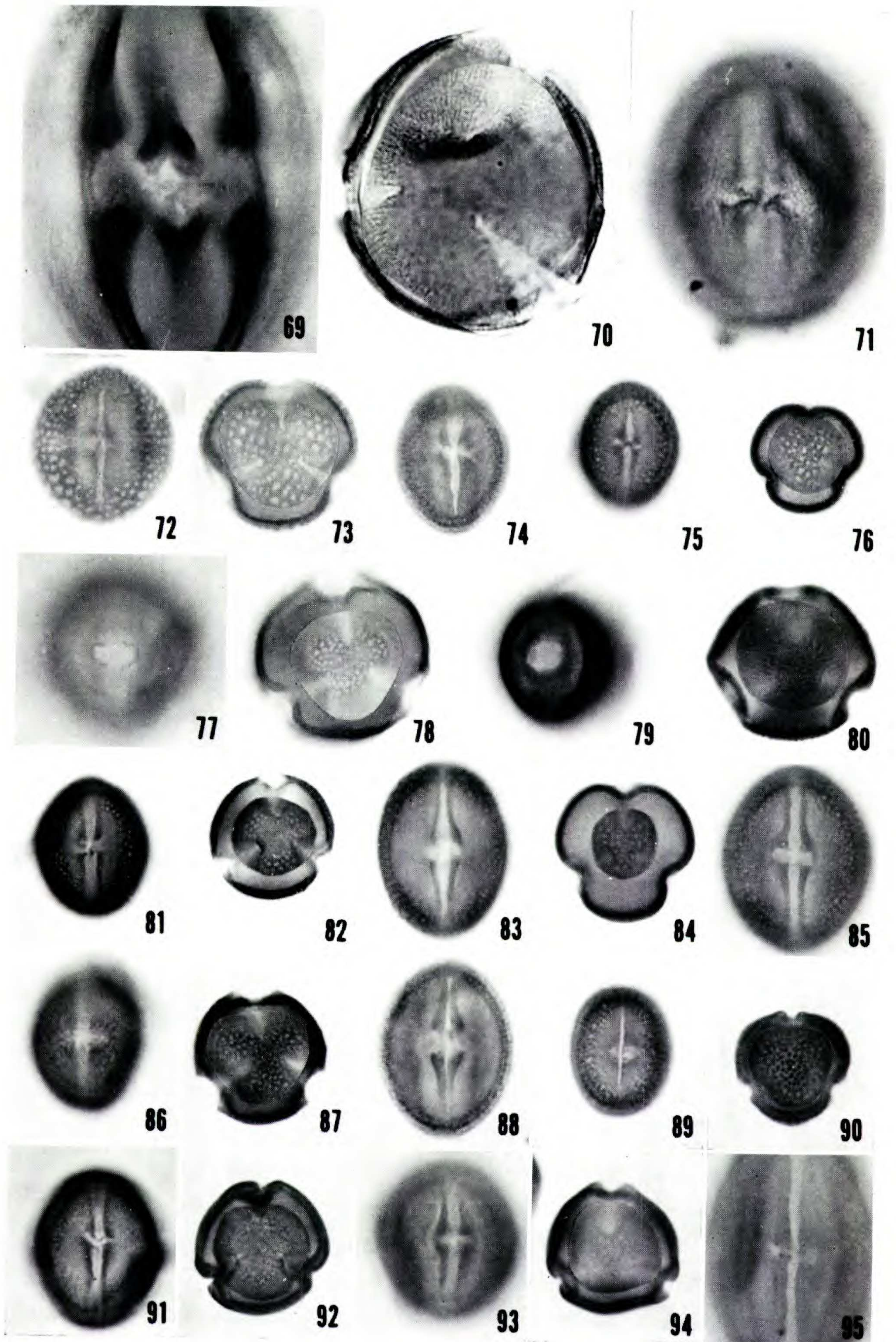
Specimen examined: *B. leprosipes* (Clos) Merr.—Sumatra, *Toroës* 3329 (US).

Flacourtia L'Herit. Figs. 74–76.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen $0.8\text{--}1.5\mu$. Exine thickness $1\text{--}1.5\mu$. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Average size: $P = 15\text{--}25\mu$; $E = 13\text{--}20\mu$.

Specimens examined: *F. euphlesia* Merr.—Philippines, *Burnea* 28968 (US). *F. indica* (Burm. f.) Merr.—Cuba, *Jack* 4961 (US). *F. mollis* Hook & Grev.—Burma, *Rock* 2158 (US). *F. ramontchii* L'Herit.—India, *Loelz* 4234 (US). Tanagerjika, *Schlieben* 5465 (US). *F. rukam* Zoll.—Sumatra, *Bartlett* 8714 (US). *F. sepiaria* Roxb.—Philippines, *Ramos* 3317 (US). *F. subintegra* A. C. Sm.—Fiji, *Smith* 6793 (US).

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optical cross section and verrucate polar surface.—62–63. *Hydnocarpus calophylla* (Jacobs 5181).—62. Equatorial view with colpus and pore.—63. Polar view, optical cross section and coarsely reticulate, simplibaculate polar surface.—64–66. *Ryparosa wrayi* (Bartlett 8410).—64. Polar view, optical cross section, bicolpate, and polar surface.—65. Equatorial view with pore.—66. Equatorial view with pore.—67–68. *Pangium edule* (Brass 27673A).—67. Equatorial view with pore.—68. Polar view, optical cross section and polar surface.



Dovyalis E. Mey. ex Arn. Figs. 77-78.

Pollen grains spheroidal, tectate, reticulate, lumen $0.8-2.0\mu$. Exine thickness 1.2μ . Tricolporate, weakly costate, endoapertures equatorially elongate. Average size: $P = 25-28\mu$; $E = 23-25\mu$.

Specimen examined: *D. abyssinica* (A. Rich.) Warb.—Kenya, *Geesteranus* 5361 (US).

Aphloia Benn. Figs. 79-80.

Pollen grains spheroidal, interhexagonal to spherical in polar view, intectate, striate, lumen 0.8μ . Exine thickness $1.5-2\mu$. Tricolporate with large elliptical, equatorially elongate endoapertures. Colpi diffuse, weakly costate. Average size: $P = 20-25\mu$; $E = 20-25\mu$.

Specimen examined: *A. theaeformis* subsp. *madagascariensis* var. *minima* (Bak.) H. Perr.—Madagascar, *Humbert* 6175 (US).

Azara Ruiz & Pav. Figs. 81-82.

Pollen grains prolate, tectate, reticulate, lumen $0.8-1.5\mu$. Exine thickness $1.5-2\mu$. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Scattered costal thickenings in the vicinity of the endoapertures in some specimens. Average size: $P = 18-25\mu$; $E = 15-20\mu$.

Specimens examined: *A. bergii* Phil.—Chile, *Claude-Joseph* 1445 (US). *A. integrifolia* Ruiz & Pav.—Chile, *Werdermann* 1386 (US). *A. lanceolata* Hook. f.—Chile, *Claude-Joseph* 2411 (US). *A. serrata* Ruiz & Pav.—Chile, *Rose* 19366 (US).

Xylosma Forst f. Figs. 83-88.

Pollen grains prolate to prolate-spheroidal, tectate, reticulate, lumen $0.5-1.5\mu$. Exine thickness $1-2\mu$. Tricolpor(-oid-)ate, costate, endoapertures equatorially

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FIGURES 69-95. Pollen of Flacourtiaceae, tribes Pangieae and Flacourtieae, $\times 1000$.—69-71. Pangieae.—69-70. *Kiggelaria africana* (*Schlieben* 7341).—69. Equatorial view with pore and costae.—70. Polar view, optical cross section and polar surface.—71. *K. integrifolia* (*Ecklon & Zeyler s. n.*), equatorial view.—72-95. Flacourtieae.—72-73. *Bennettiodendron leprosipes* (*Toroës* 3329).—72. Equatorial view with colpus.—73. Polar view, optical cross section and reticulate polar surface.—74. *Flacourtia euphlexia* (*Burnea* 28986), equatorial view with colpus and pore.—75-76. *F. rukam* (*Bartlett* 8714).—75. Equatorial view with colpus.—76. Polar view, optical cross section and reticulate polar surface.—77-78. *Dovyalis abyssinica* (*Geesteranus* 5361).—77. Equatorial view with pore.—78. Polar view, optical cross section with reticulate polar surface.—79-80. *Aphloia theaeformis* (*Humbert* 6175).—79. Equatorial view with pore.—80. Polar view, optical cross section and polar surface.—81-82. *Azara bergii* (*Claude-Joseph* 1445).—81. Equatorial view with colpus.—82. Polar view, optical cross section and finely reticulate polar surface.—83-84. *Xylosma fawcettii* (*Britton* 1311).—83. Equatorial view with colpus.—84. Polar view, optical cross section and polar surface.—85. *X. spiculiferum* (*Schiefer* 593), equatorial view with colpus and pore.—86-87. *X. luzonensis* (*Ramos & Deroy* 22579).—86. Equatorial view with colpus.—87. Polar view, optical cross section and polar surface.—88. *X. hawaiiense* (*Hitchcock* 15280), equatorial view with colpus and costae.—89-90. *Poliothyrsis sinensis* (*Wilson* 500).—89. Equatorial view with colpus and pore.—90. Polar view, optical cross section and polar surface.—91-92. *Carrieria calycina* (*Wilson* 1104).—91. Equatorial view with colpus and pore.—92. Polar view, optical cross section and polar surface.—93-94. *Itoa stapfii* (*Hoogland* 5079).—93. Equatorial view with colpus and pore.—94. Polar view, optical cross section and polar surface.—95. *I. orientalis* (*Henry* 10703), equatorial view with colpus and pore.

elongate, distinct, with diffuse ends. Colpi and endoapertures may be constricted. Sculpturing elements occasionally found on colpi membranes when endoapertures absent. Average size: $P = 18-25\mu$; $E = 15-25\mu$.

Specimens examined: *X. blepharodes* Lundell—Texas, *Barber 14a* (US). *X. ciliatifolium* (Clos) Eichl.—Brazil, *Pickel 3221* (US). *X. fawcettii* Urb.—Jamaica, *Britton 1311* (US). *X. flanganii* Bolus—Pretoria, *Flangan 682* (US). *X. flexuosa* Hemsl.—Guatemala, *Skutch 348* (US). *X. hawaiiense* Seem.—Hawaii, *Hitchcock 15280* (US). *X. longifolium* Clos—China, *Henry 12635* (US). *X. luzonensis* (Presl) Clos—Philippines, *Ramos & Deroy 22579* (US). *X. orbiculata* Forst.—Tonga, *Yunker 16235* (US). *X. racemosum* Miq.—China, *Levine 1816* (US). *X. spiculiferum* (Yul.) Tr. & Pl.—Colombia, *Schiefer 593* (US). *X. venosum* N. E. Br.—Argentina, *Schwarz 475* (US).

Poliothyrsis Oliv. Figs 89–90.

Pollen grains prolate, tectate, reticulate, lumen $0.5-1\mu$. Exine thickness 2.5μ . Tricolporate, costate, endoapertures equatorially elongate. Average size: $P = 18-20\mu$; $E = 15-18\mu$.

Specimen examined: *P. sinensis* Oliv.—China, *Wilson 500* (US).

Carrierea Franch. Figs. 91–92.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ . Exine thickness 1.3μ . Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate, irregular. Average size: $P = 23-25\mu$; $E = 18-20\mu$.

Specimen examined: *C. calycina* Franch.—China, *Wilson 1104* (US).

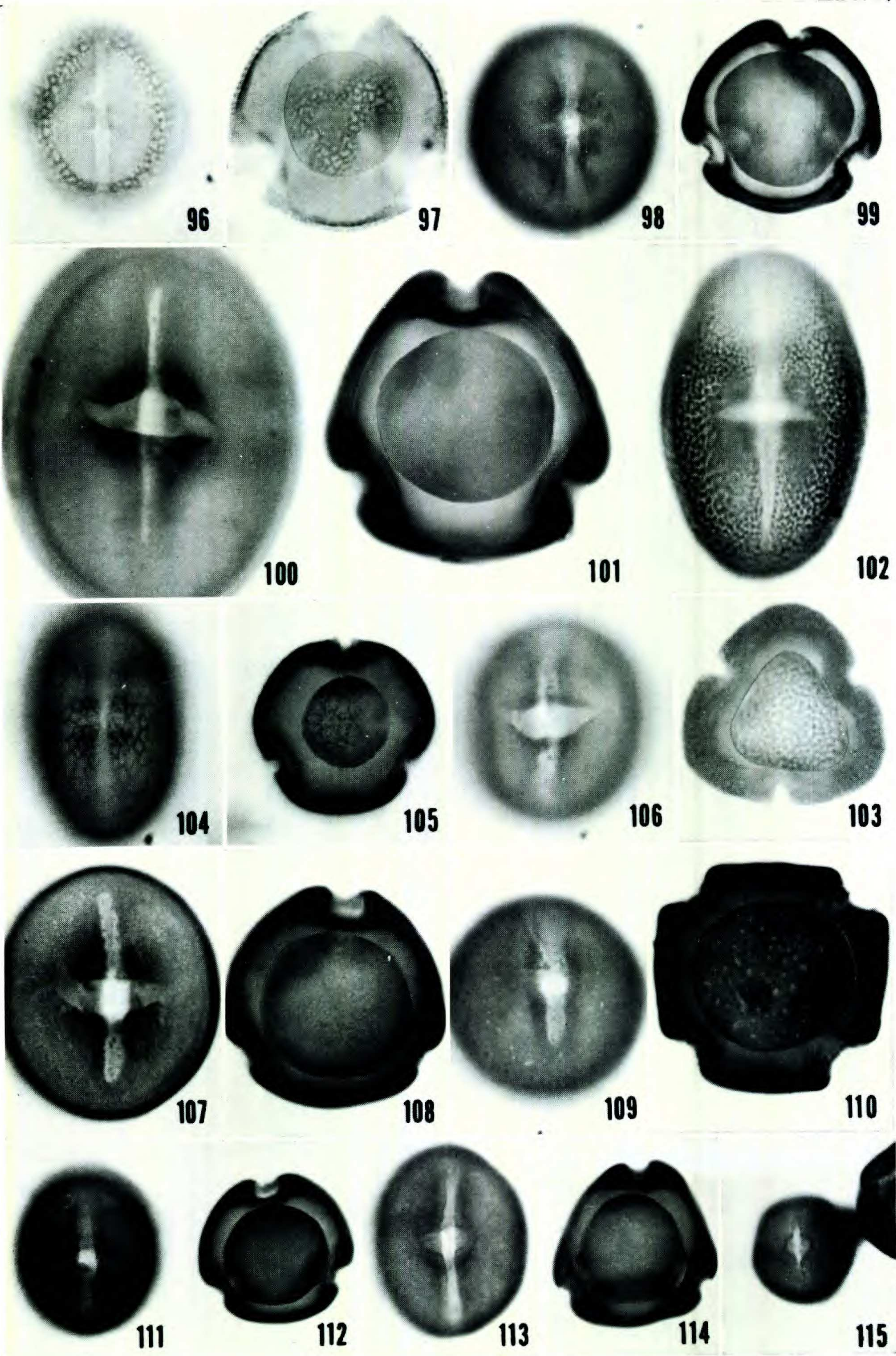
Itoa Hemsl. Figs. 93–95.

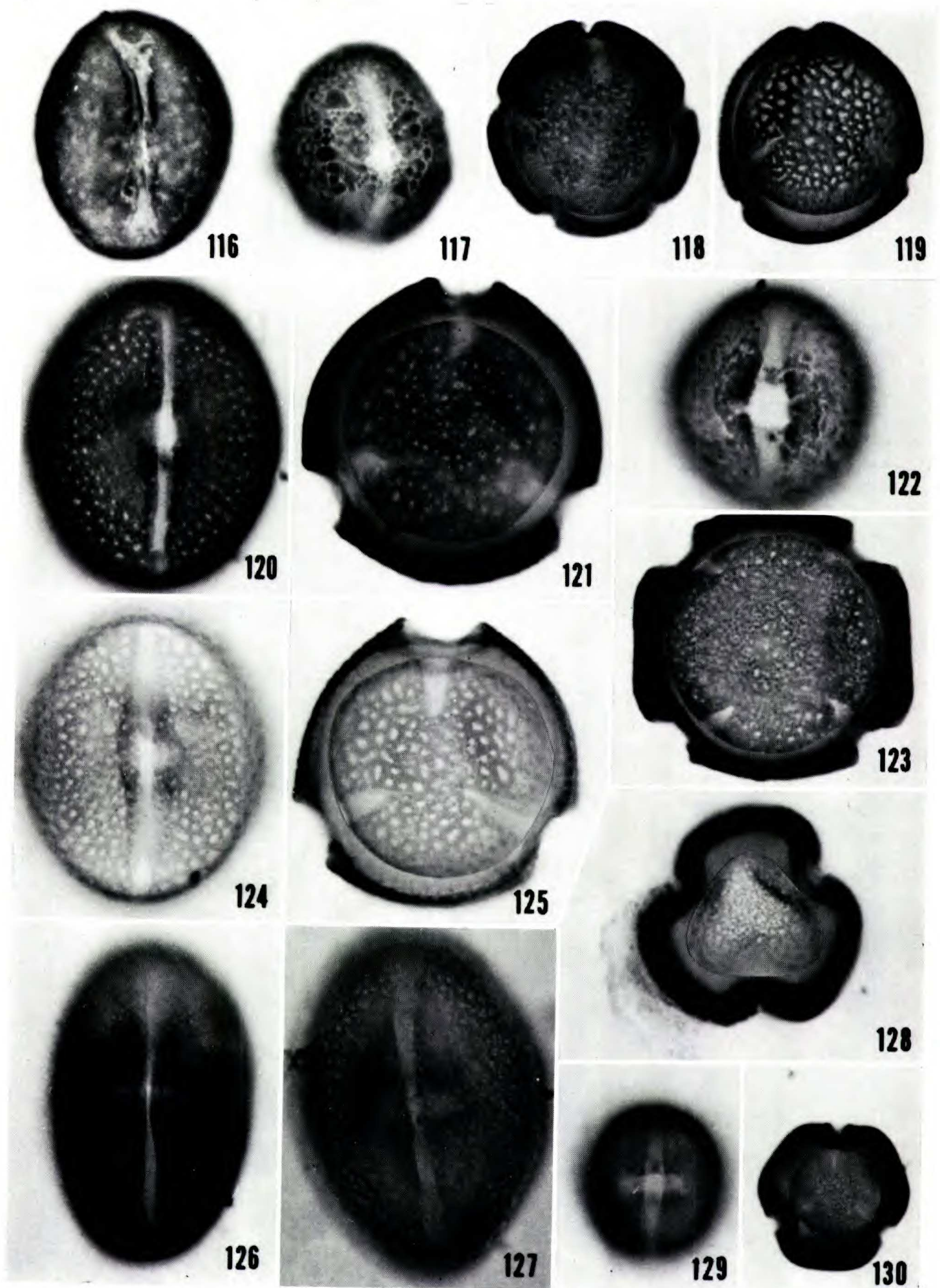
Pollen grains prolate-spheroidal, tectate, reticulate, lumen $0.5-1\mu$. Exine thickness $1-1.5\mu$. Tricolporate, costate, endoapertures equatorially elongate with diffuse ends. Average size: $P = 18-43\mu$; $E = 15-30\mu$.

Specimens examined: *I. orientalis* Hemsl.—China, *Henry 10703* (US). *I. stapfii* (Koord.) Sleum.—New Guinea, *Hoogland 5079* (US).

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FIGURES 96–115. Pollen of Flacourtiaceae, tribes Flacourtieae and Casearieae, $\times 1000$.—96–97. Flacourtieae. *Idesia polycarpa* (Forest 17558).—96. Equatorial view with colpus.—97. Polar view, optical cross section and reticulate polar surface.—98–115. Casearieae.—98–99. *Casearia graveolens* (Rock 2839).—98. Equatorial view with colpus.—99. Polar view, optical cross section, and polar surface.—100–101. *C. cambessedessii* (Haught 2828).—100. Equatorial view of interior surface, pore and colpus.—101. Polar view, optical cross section and polar surface.—102–103. *C. javitensis* (Killip & Smith 30153).—102. Equatorial view, pore and colpus.—103. Polar view, optical cross section and polar surface.—104–105. *C. floribunda* (Gossweiler 718).—104. Equatorial view.—105. Polar view, optical cross section and polar surface.—106. *C. tomentosa* (Stewart 13756), equatorial view of interior surface, pore and colpus.—107–108. *C. aculeata* (Rouirosa 568).—107. Equatorial view of interior surface, pore and colpus.—108. Polar view, optical cross section and polar surface.—109–110. *C. bahamensis* (Britton, Cowell & Earle 10300).—109. Equatorial view colpus and pore.—110. Polar view, optical cross section of tetracolporate grain and polar surface.—111–112. *C. fuliginosa* (Cuming 1240).—111. Equatorial view.—112. Polar view, optical cross section and polar surface.—113–114. *C. disticha* (Degener & Ordonez 13588).—113. Equatorial view, colpus and pore.—114. Polar view, optical cross section and polar surface.—115. *C. aequilateralis* (Lau 39), equatorial view with colpus and pore.





FIGURES 116-130. Pollen of Flacourtiaceae, tribe Casearieae, $\times 1000$.—116-118. *Gossypiospermum eriophorum* (Jack 4970).—116. Equatorial view with indeterminate colpus.—117. Equatorial view showing grain with verrucate-rugulate surface.—118. Polar view, optical cross section and polar surface of pentaperturate grain.—119. *Laetia procera* (Ekman 12380), polar view, optical cross section and reticulate polar surface.—120-121. *L. apetala* (Hassler 7515).—120. Equatorial view with colpus and pore.—121. Polar view, optical cross section

Idesia Maxim. Figs. 96–97.

Pollen grains prolate-spheroidal, semitectate, reticulate, lumen $1-2\mu$. Exine thickness 1.5μ . Tricolporoidate, costate, endoapertures often absent due to constricted colpi at equator. Average size: $P = 23-28\mu$; $E = 20-25\mu$.

Specimen examined: *I. polycarpa* Maxim.—China, *Forrest 17558* (US).

CASEARIEAE

Casearia Jacq. Figs. 98–115.

Pollen grains spheroidal to prolate, polar view circular to semiangular, semitectate to tectate, psilate to mostly reticulate or per-reticulate, lumen $0.3-4\mu$. Exine thickness $1-3\mu$. Tri(-4-)colporate, endoapertures equatorially elongate with pointed ends, costate. Average size: $P = 18-58\mu$; $E = 18-45\mu$.

Specimens examined: *C. aculeata* Jacq.—Mexico, *Rouirosa 568* (US). *C. aequilateralis* Merr.—China, *Lau 39* (US). *C. arborea* (L. C. Rich.) Urb.—Cuba, *Webster 4082* (US). *C. arguta* H. B. K.—Chile, *Sargent 27* (US). *C. bahamensis* Urb.—Cuba, *Britton, Cowell & Earle 10300* (US). *C. blanchetiana* Miq.—Peru, *Klug 2294* (US). *C. boliviana* Briq.—Bolivia, *Britton & Rusby 2421* (US). *C. cambessedesii* Eichl.—Columbia, *Haught 2828* (US). *C. celastroides* Kl.—British Guiana, *Smith 2449* (US). *C. cineria* Turcz.—Philippines, *Cabibe 5* (US). *C. comocladifolia* Vent.—Haiti, *Miller 276* (US). *C. corymbosa* H. B. K.—Columbia, *Dugand 6890* (US). *C. decandra* Jacq.—Puerto Rico, *Britton, Stevens & Hess 2387* (US). *C. dinklagei* Gilg—Liberia, *Cooper 408* (US). *C. disticha* A. Gray—Fiji, *Degener & Ordonez 23588* (US). *C. fasciculata* (R. & P.) Sleum.—Brazil, *Krukoff 6488* (US). *C. floribunda* (Mart.) Burret—Congo, *Gossweiler 718* (US). *C. fuliginosa* Blco.—Philippines, *Cuming 1240* (US). *C. grandiflora* Camb.—Brazil, *Ducke 80* (US). *C. graveolens* Dalz.—China, *Rock 2839* (US). *C. guianensis* (Aubl.) Urb.—Panama, *Paul 606* (US). *C. hirsuta* Sw.—West Indies, *Curtiss 310* (US). *C. hosei* Merr.—North Borneo, *Villamil 355* (US). *C. inaequilateria* Camb.—Brazil, *Smith & Reitz 9646* (US). *C. javitensis* H. B. K.—Brazil, *Killip & Smith 30153* (US). *C. nitida* Jacq.—Mexico, *Hinton 15803* (US). *C. obovata* Schlecht.—Mexico, *Matuda 4437* (US). *C. odorata* Macf.—Jamaica, *Harris 9808* (US). *C. ophitcola* M. Vict.—Cuba, *Figueiras 1261* (US). *C. pringlei* Briq.—Mexico, *McVaugh 10216* (US). *C. sylvestris* Sw.—Colombia, *Klug 1720* (US). Costa Rica, *Smith 1003* (US). *C. tomentosa* Roxb.—India, *Stewart 13756* (US).

Gossypiospermum Urb. Figs. 116–118.

Pollen grains prolate to prolate-spheroidal, semitectate, rugulate-reticulate, lumen 0.3μ . Exine thickness 1.3μ . Apertures 3, 4, 5-colporate in equal quantities, costate, colpi may be branched often with ragged edges and indeterminate ends; often very diffuse. Average size: $P = 28-33\mu$; $E = 23-28\mu$.

Specimen examined: *G. eriophorum* (C. Wr.) Urb.—Cuba, *Jack 4970* (US).

Laetia Loefl. ex L. Figs. 119–123.

Pollen grains subprolate, tectate, reticulate to occasionally rugulate, lumen

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and polar surface of semitectate grain.—122–123. *L. thamnia* (Lundell 7430).—122. Equatorial view with colpus and pore surrounded by a rugulate exine.—123. Polar view, optical cross section and semitectate polar surface.—124–125. *Hecatostemon quazumiifolius* (Smith 174).—124. Equatorial view.—125. Polar view, optical cross section and reticulate polar surface.—126. *Ryania speciosa* (Cuatrecasas 6847), equatorial view with colpus and pore.—127–128. *R. canescens* (Prance, Silva & Pires 59148).—127. Equatorial view, colpus and pore.—128. Polar view, optical cross section and polar surface.—129–130. *Zuelania roussovieae* (Purpus 10703).—129. Equatorial view, colpus and pore.—130. Polar view, optical cross section and polar surface.

1–4 μ . Exine thickness 1.3–2.3 μ . Apertures 3, 4-colporate, costate, ends of colpi often indeterminate, ends diffuse. Average size. P = 25–40 μ ; E = 25–35 μ .

Specimens examined: *L. apetala* Jacq.—Paraguay, Hassler 7515 (US). *L. procera* (Poepp. & Endl.) Endl.—Hispaniola, Ekman 12380 (US). *L. suaveolens* (P. & E.) Bth.—Peru, Klug 1443 (US). *L. thamnia* L.—Mexico, Lundell 7430 (US).

Hecatostemon Blake Figs. 124–125, 171–172.

Pollen grains prolate-spheroidal, semitectate, reticulate, duplibaculate, lumen 1–3 μ . Exine thickness 2 μ . Tricolporate, costate, endoapertures equatorially elongate, ends diffuse. Grains often appearing anisopolar due to proliferations of ektexine over colpi membranes on one side of ora. Average size: P = 35–42 μ ; E = 30–38 μ .

Specimens examined: *H. guazumifolius* (H. B. K.) Sleum.—Venezuela, Smith 174 (US).

Ryania Vahl Figs. 126–128.

Pollen grains prolate, tectate, reticulate, simplibaculate, lumen 0.3–1 μ . Exine thickness 2 μ . Tricolporate, endoapertures equatorially elongate. Average size: P = 35–48 μ ; E = 23–33 μ .

Specimens examined: *R. angustifolia* (Turcz.) Monach.—Brazil, Holt & Gehringer 380 (US). *R. canescens* Eichl.—Brazil, Prance, Silva & Pires 59148 (US). *R. speciosa* var. *chocoensis* (Tr. & Pl.) Monach.—Columbia, Cuatrecasas 6847 (US).

Zuelania A. Rich. Figs. 129–132.

Pollen grains prolate, tectate, finely reticulate or psilate, lumen 0.3 μ or absent. Exine thickness 1.5–2 μ . Apertures 3, 4-colporate, costate, endoapertures equatorially elongate. Average size: P = 28–38 μ ; E = 28–35 μ .

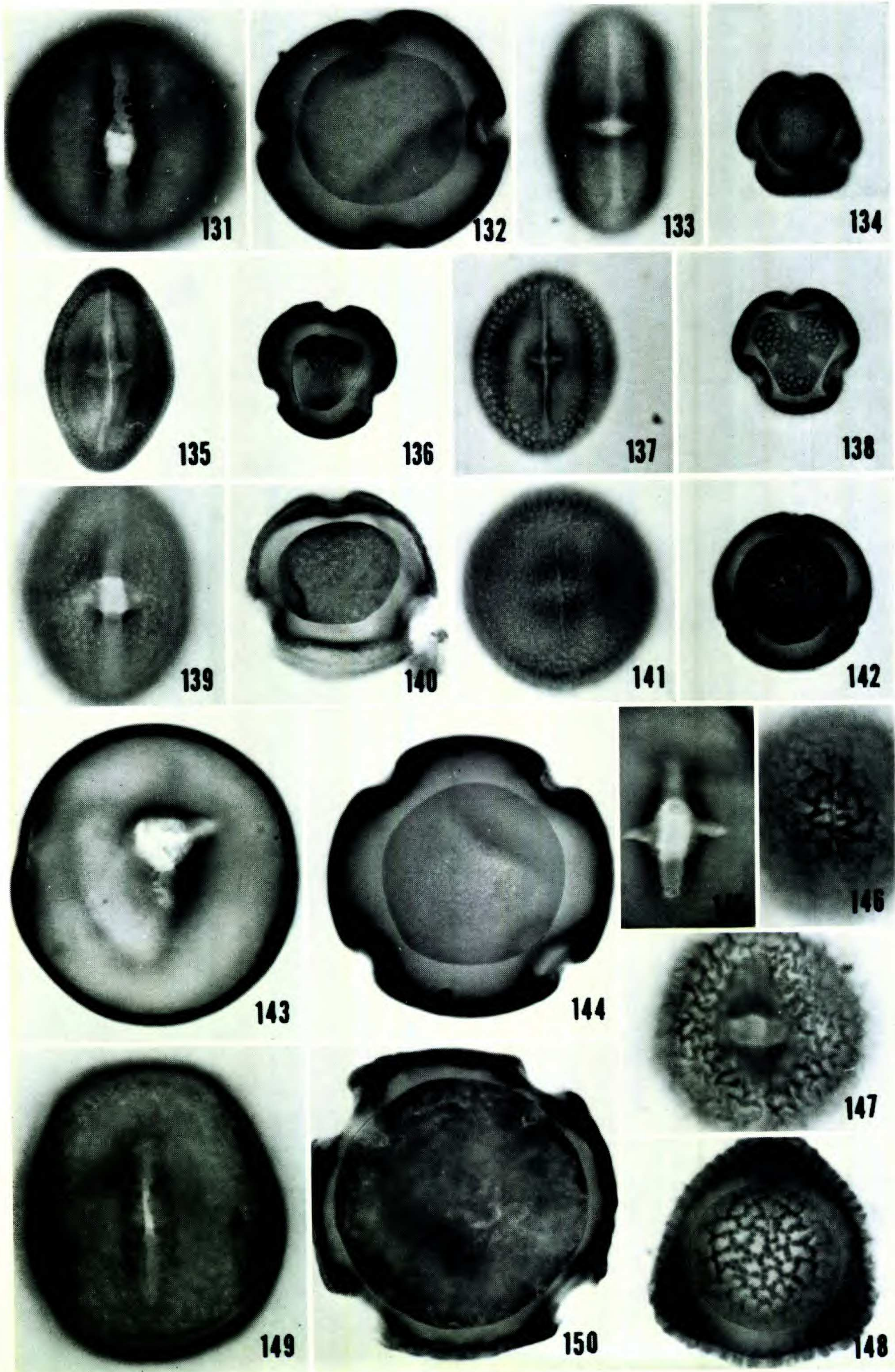
Specimens examined: *Z. guidonia* (Sw.) Britton & Millsp.—Mexico, Purpus 10703 (US), Enriquez 567 (US).

Osmelia Thwaites Figs. 133–134.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5 μ . Exine thickness 1–1.5 μ . Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: P = 20–33 μ ; E = 13–23 μ .

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FIGURES 131–150. Pollen of Flacourtiaceae, tribe Casearieae, \times 1000.—131–132. *Zuelania guidonia* (Enriquez 567).—131. Equatorial view, colpus and pore.—132. Polar view, optical cross section and polar surface.—133–134. *Osmelia bartlettii* (Krukoff 4003).—133. Equatorial view, colpus and pore.—134. Polar view, optical cross section and polar surface.—135–136. *Ophiobotrys zenkeri* (Vique 1753).—135. Equatorial view.—136. Polar view, optical cross section and polar surface.—137–138. *Lunania mexicana* (Purpus 7776).—137. Equatorial view, colpus and pore.—138. Polar view, optical cross section and polar surface.—139–140. *Euceraea nitida* (Fernandez s. n.).—139. Equatorial view, colpus and pore.—140. Polar view, optical cross section and polar surface.—141–142. *Tetrathylacium macrophyllum* (Woytkowski 7634).—141. Equatorial view.—142. Polar view, optical cross section and polar surface.—143–145. *Samyda yucatanensis* (Lundell 7338).—143. Equatorial view, reduced aperture.—144. Polar view, optical cross section and polar surface.—145. Equatorial view of aperture, shortened colpus and lalongate pore.—146–148. *Neoptychocarpus apodanthus* (Ducke 1633).—146. Equatorial view of colpus and margin.—147. Equatorial view, internal surface of pore.—148. Polar view, optical cross section and reticulate, simplibaculate polar surface.—149–150. *Samyda dodecandra* (Sargent 652).—149. Equatorial view, colpus.—150. Polar view, optical cross section and polar surface.



Specimens examined: *O. bartlettii* Merr.—Sumatra, *Krukoff* 4003 (US). *O. maingayi* King—Malaya, *Kochummes* 75982 (US). *O. philippinensis* Benth.—Philippines, *Ahern* 133 (US).

Ophiobotrys Gilg Figs. 135–136.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ . Exine thickness $1.5\text{--}2\mu$. Tricolporate, costate, endoapertures equatorially elongate, often with pointed ends. Occasional ektexine elements above endoapertures on colpi membranes. Average size: $P = 28\text{--}30\mu$; $E = 18\text{--}20\mu$.

Specimen examined: *O. zenkeri* Gilg—Ghana, *Vique* 1753 (US).

Lunania Hook. Figs. 137–138.

Pollen grains prolate, tectate, reticulate, lumen $1\text{--}3\mu$. Exine thickness 1.5μ . Tricolporate, costate, endoapertures equatorially elongate with blunt or usually pointed ends. Average size: $P = 18\text{--}25\mu$; $E = 13\text{--}18\mu$.

Specimens examined: *L. mexicana* Brandeg.—Mexico, *Purpus* 7776 (US). *L. parviflora* Spruce ex Benth.—Peru, *Wurdack* 1820 (US), *Vargas* 17785 (US).

Euceraea Mart. Figs. 139–140.

Pollen grains are prolate, tectate, reticulate, simplibaculate, lumen 1μ . Exine thickness 1μ . Tricolporate, costate, endoapertures equatorially elongate, oval. Average size: $P = 30\text{--}33\mu$; $E = 23\text{--}25\mu$.

Specimen examined: *E. nitida* Mart.—Colombia, *Fernandez s. n.* (US).

Tetrathylacium Poepp & Endl. Figs. 141–142.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen 0.5μ . Exine thickness $1\text{--}2.5\mu$. Tricolporate, costate, colpi short, narrow, endoapertures equatorially elongate with blunt, indeterminate ends. Average size: $P = 20\text{--}28\mu$; $E = 20\text{--}25\mu$.

Specimens examined: *T. costaricense* Stand.—Costa Rica, *Skutch* 4281 (US). *T. macrophyllum* P. & E.—Peru, *Woytkowski* 7634 (US).

Samyda Jacq. Figs. 143–145, 149–150.

Pollen grains prolate-spheroidal, tectate, reticulate to rugulate, lumen $0.3\text{--}0.7\mu$. Exine thickness $1.5\text{--}2\mu$. Apertures 4, 5-colporate, costate, placement of apertures often irregular, off the equator and diagonal to the meridian. Colpi often reduced or fragmented. Endoapertures elliptical meridianally with constricted pointed ends, equatorially elongate extensions give a cross shape to the endoaperture. Some ektexine elements on colpi membranes. Average size: $P = 30\text{--}40\mu$; $E = 30\text{--}40\mu$.

Specimens examined: *S. dodecandra* Jacq.—Puerto Rico, *Sargent* 652 (US). *S. yucatanensis* Standl.—Mexico, *Lundell* 7338 (US).

Neoptychocarpus Buchheim Figs. 146–148.

Pollen grains spheroidal or prolate spheroidal, semiangulaperturate in polar view, semitectate, per-reticulate, simplibaculate, lumen $4\text{--}5\mu$. Exine thickness 2.5μ . Tricolporate, costate, endoapertures equatorially elongate and elliptical. Average size: $P = 28\text{--}30\mu$; $E = 28\text{--}30\mu$.

Specimen examined: *N. apodanthus* (Kuhl.) Buchheim—Brazil, *Ducke 1633* (US).

Abatia Ruiz & Pavon Figs. 151–156.

Pollen grains prolate to prolate-spheroidal, tectate, finely reticulate, lumen 0.5μ . Exine thickness $1.5\text{--}2\mu$. Tricolporate, endoapertures equatorially elongate, costate, ectexine elements occasionally on the colpi membranes above and below endoapertures. Average size: $P = 18\text{--}30\mu$; $E = 15\text{--}30\mu$.

Specimens examined: *A. borealis* L. O. Wms.—Costa Rica, *Lankester 674* (US). *A. parviflora* R. & P.—Colombia, *Fosberg & Villareal 20577* (US). *A. spicata* (Turcz.) Sleum.—Peru, *Bingham 2067* (US). *A. tomentosa* Mart.—Brazil, *Barreto 19905* (US).

Aphaerema Miers Figs. 157–158.

Pollen grains prolate, tectate, finely reticulate, lumen 0.3μ . Exine thickness 1.5μ . Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: $P = 18\text{--}20\mu$; $E = 15\text{--}18\mu$.

Specimen examined: *A. spicata* Miers—Brazil, *Klein 444* (US).

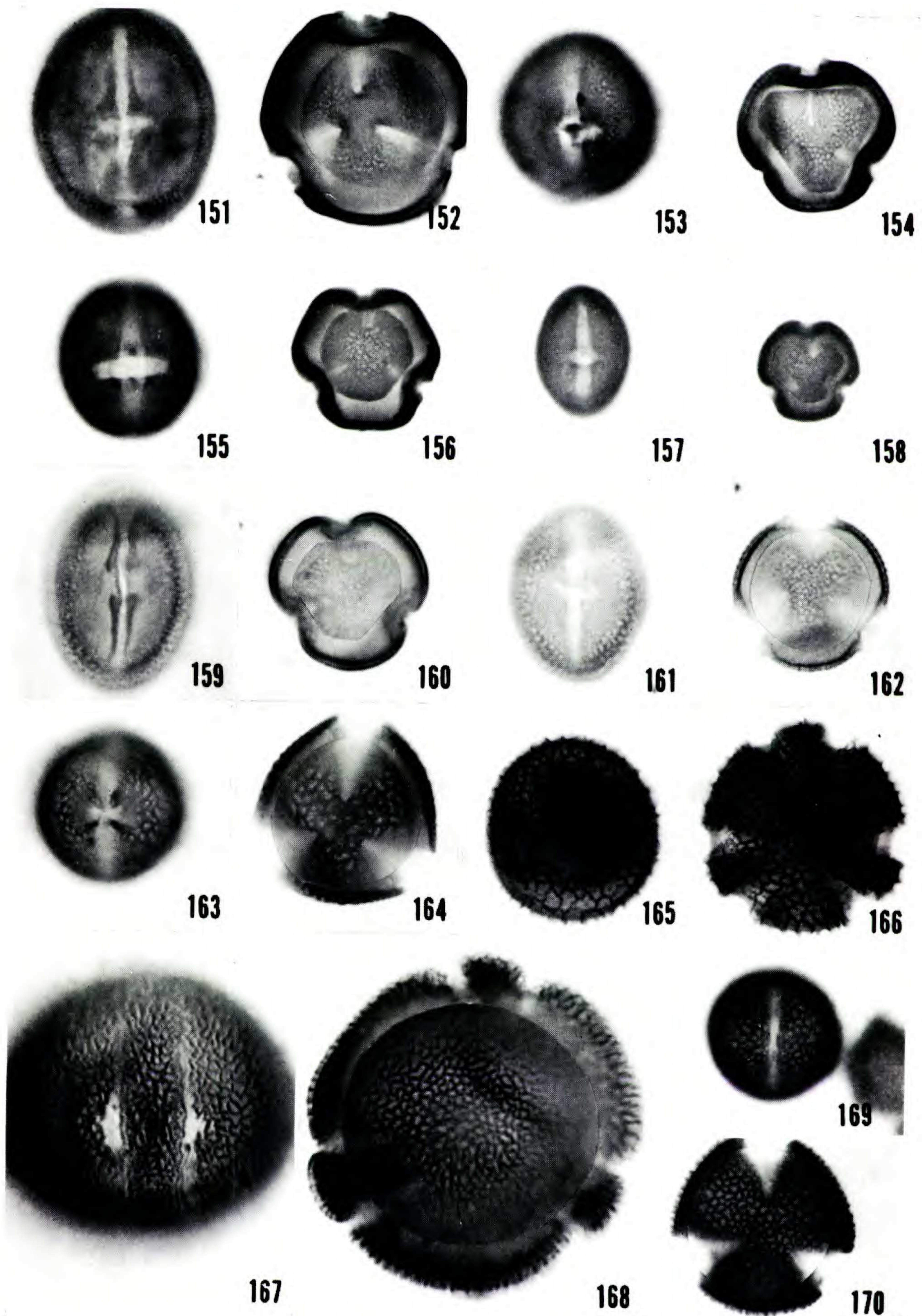
LEVEL OF ADVANCEMENT

Traditionally, comparative morphologists state that the only trend of specialization anchored in the fossil record is that of tracheary tissue. Recent pollen analysis from carefully dated Mesozoic and Cenozoic strata, however, have added another order of precision to our knowledge of evolutionary specialization of the angiosperms (Brenner, 1967; Doyle, 1969; Muller, 1970).

In schemes depicting the earliest evolution of dicotyledonous pollen, triaperturate pollen is considered relatively specialized (Muller, 1970; Kuprianova, 1967, 1969; Nair, 1965). However, in surveys of the complete range of modern dicotyledonous pollen types, the small, reticulate, tricolpate and tricolporate types form the basis for considerable further specialization and elaboration. This kind of pollen is represented in Cenomanian strata (Brenner, 1967).

In his study of the Cretaceous pollen record of the Atlantic coast, Doyle (1969) found a statistical trend in the triaperturate type which included tricolpate, tricolporoidate, tricolporate and triporate pollen in successively higher levels. The earliest grains were prolate or subspheroidal, retipilate or reticulate, occurred as single grains, and were small in size. In the evolution of the triaperturate type, many genera of Flacourtiaceae are primitive in all criteria.

While the affinities of these early pollen types are uncertain, it has been suggested that grains of Polycarpicidae, Amentiferae and Cistiflorae are represented (Muller, 1970). Specialized trends as found in the Theales make the identification of those pollen types from early strata less tentative. Many early Cretaceous pollen grains have been assigned to Dilleniaceae, Ochnaceae, Salicaceae, and Columniferae. Despite the fact that pollen of many extant genera of Flacourtiaceae are indistinguishable from pollen occurring in the above mentioned families, the earliest pollen assigned to the Flacourtiaceae is from the upper Miocene (Muller, 1970). It seems probable that earlier pollen of Flacourtiaceae has been misidentified due to lack of knowledge of the family. Previous statistical correlations between vegetative and floral features have placed the Flacourtiaceae among the most primitive of angiosperm families (Sporne, 1954).



FIGURES 151-170. Pollen of Flacourtiaceae and certain excluded genera, tribes Casearieae, Prockieae, and Paropsieae, $\times 1000$.—151-158. Casearieae.—151-152. *Abatia borealis* (Lankester 674).—151. Equatorial view.—152. Polar view, optical cross section and polar surface.—153-154. *A. parviflora* (Fosburg & Villareal 20577).—153. Equatorial view.—154.

Many genera of Flacourtiaceae have pollen that conform to the criteria of wind pollination as defined by Whitehead (1969). These include production and release of numerous grains, exposed anthers and stigmas, grain diameter 20–40 μ , thin exines and a smooth surface. Considerably more observations are needed in this family before the relation between pollen morphology and mechanisms of pollination can be adequately discussed. Detailed studies of the records of several families indicate that pollen evolution is concurrent with taxonomic diversification (Muller, 1970). This should prove to be the case in the Flacourtiaceae.

SUMMARY OF INTRAFAMILIAL RELATIONSHIPS

The tribes Berberidopsidae and Oncobae do not appear sharply defined from each other. While the grains of the Berberidopsidae are small to medium-sized, some of the largest grains in the family are found in *Mayna* and *Carpotroche* of the Oncobae. Both tribes have a tendency toward high, equatorially elongate, rectangular endoapertures. The tricolpate pollen of *Berberidopsis* is the most primitive of the family.

Sculpturing varies in these tribes from psilate to coarsely reticulate. Some treatments of the family (Bamps, 1968; Gilg, 1925) do not separate the two tribes, leaving all genera in the Oncobae. The limited pollen sample of this study, while diverse, does not clearly show a separation along tribal lines as suggested by Hutchinson (1967).

The tribes Scolopieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. The tribe Prockieae, assigned by Hutchinson to the Tiliaceae, could easily be added to this group. All have costate colpi, a wide or narrow endoaperture, and a reticulate or finely reticulate exine. Costae in the Homalieae tend to be abbreviated. In *Homalium* and *Dissomeria*, the costae are concentrated at the four corners of the intersection formed by the endo- and ectoapertures. In some *Homalium* specimens, the costae only define the margins of the endoapertures. It is doubtful if keys to the pollen of most of these genera could be made without electron microscope preparations of the wall. One specimen labelled *Banara costaricensis* (Standl.) Sleumer (Figs. 44–45) is about twice as large as any other known *Banara* specimen. In aperture morphology and sculpturing, it most closely resembles pollen of the genus *Casearia*.

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Polar view, optical cross section and polar surface.—155–156. *A. spicata* (Bingham 2067).—155. Equatorial view.—156. Polar view, optical cross section and polar surface.—157–158. *Aphaerema spicata* (Klein 444).—157. Equatorial view.—158. Polar view, optical cross section and polar surface.—159–162. Prockieae.—159–160. *Hasseltia lateriflora* (Smith 1915).—159. Equatorial view.—160. Polar view, optical cross section and polar surface.—161–162. *Prockia crucis* (Hinton 4277).—161. Equatorial view.—162. Polar view, optical cross section and polar surface.—163–170. Paropsieae.—163–164. *Soyauxia floribunda* (Straub 107).—163. Equatorial view.—164. Polar view, optical cross section and reticulate polar surface.—165–166. *Smeathmannia pubescens* (Straub 117).—165. Equatorial view.—166. Polar view, reticulate, hexacolpate grain.—167–168. *Paropsiopsis pulchra* (Zenker 413).—167. Equatorial view, pair of colporate apertures.—168. Polar view, optical cross section and polar surface of hexacolpate grain.—169–170. *Ancistrothyrsis tessmannii* (Ducke 24387).—169. Equatorial view.—170. Polar view, optical cross section and reticulate polar surface.

Some of the genera of Caseariae resemble the previous group of four tribes but add more specialized trends. These include greater size, more frequent 4–5 aperturate grains, and wide elongate endoapertures with pointed ends (*Casearia*). Some per-reticulate grains (*Neoptychocarpus*) and breviaperturate grains (*Samyda*) are also found. Thicker, unsculptured and unstructured exines are found in *Casearia*.

The Pangieae are isolated and have a number of different specialized features in different genera. Among these are brevicolpate to porate apertures (*Pangium*, *Ryparosa*), large grains with per-reticulate sculpturing (*Hydnocarpus*), rugulate sculpturing (*Trichadenia*), thick, conspicuously costate exines (*Kiggelaria*), and medium to large size in all specimens examined.

The Paropsieae are as isolated from the other tribes in their pollen morphology as are the Pangieae. Their sculpturing pattern is per-reticulate of the simplibaculate type and is separable from the other tribes on this appearance. This sculpturing pattern most closely resembles the per-reticulate type of the Passifloraceae rather than the perforated tectum, duplibaculate type found in the Oncobeeae (*Mayna*). The hexacolporate, paired apertures especially separate this tribe from other Flacourtiaceae.

INTERFAMILIAL RELATIONSHIPS

Although pollen provides but one set of characters which must be correlated with observations on other structures before intrageneric and familial relationships will be resolved, it remains useful to comment on the degree of resemblance of pollen of various families to that of the Flacourtiaceae. Families from eleven orders are thought to be related to a flacourtiaceous stock (Takhtajan, 1969). In the following comparison, Takhtajan's (1969) organization will be followed. Unless otherwise acknowledged, comparative pollen data is from Erdtman (1952).

Violales.—The Lacistemaceae and Stachyuraceae have been considered quite close to the Flacourtiaceae. The pollen morphology is quite supportive of this arrangement, the grains being small to medium-sized, finely reticulate, tricolporate and with equatorially elongate endoapertures.

The Violaceae are considered by Takhtajan (1969) to be linked to the Flacourtiaceae through the primitive tribe Rinoreeae. Some pollen of this family is well within the range of the Flacourtiaceae, but other tribes show increased specialization. This includes large size, up to five apertures, and protruding aperture margins.

The Bixaceae and Cochlospermaceae, considered related in most schemes, have pollen which allows separation of the two families and separation from the Flacourtiaceae (Keating, 1972; Nair, 1962*a*). Their pollen fits the range of the Flacourtiaceae, especially resembling the tribe Oncobeeae. However, cochlospermaceous and bixaceous pollen is distinct enough to make any tribal alliance uncertain. The Cistaceae have pollen quite similar to that of the Flacourtiaceae. The endoapertures are oval or circular. More specialized tendencies include larger size, striate grains, and a more complex reticulum (Heydacker, 1963; Jean & Pons, 1963).

On the basis of pollen the Violales seem to be a related group of families with the Flacourtiaceae as basic for this assemblage.

Passiflorales.—The Passifloraceae have long been considered closely allied to the Flacourtiaceae through the tribe Paropsieae (see review by DeWilde, 1971). Gilg (1925) considered the Paropsieae to be Tribe III of the Flacourtiaceae, but on the basis of pollen it forms an isolated group in the family. Pollen morphology of the tribe has been described by Spirlet (1965) and Presting (1965) with the finding that the genera agree quite closely with other Passifloraceae. Pollen of the Passifloraceae can be tricolporate, but many genera are distinctly six and twelve zonicolporate. *Paropsiopsis* (Figs. 167–168) and *Smeathmannia* (Figs. 165–166) illustrate another characteristic feature of some Passifloraceae, especially of *Passiflora*, the tendency for multiple apertures to be grouped in pairs. This highly distinctive pattern seems unquestionably to belong in the Passifloraceae. Pollen of the genera *Ancistrothyrsis* (Figs. 169–170) and *Soyauxia* (Figs. 163–164) are only tricolporate and closer to the Flacourtiaceae.

When included in the Flacourtiaceae, the tribe is distinguished by the presence of a corona; in the Passifloraceae, the tribe is distinguished by its arboreous habit (DeWilde, 1971). The evidence from pollen supports the consensus of intermediacy of the tribe, but its best placement seems to be with the Passifloraceae (Sleumer, 1970; DeWilde, 1971).

The remaining families of the Passiflorales (Turneraceae, Malesherbiaceae, Achariaceae, and Caricaceae) seem derived from the Passifloraceae on the basis of pollen and more distantly related to the Flacourtiaceae. Their pollen grains are tricolporate, tend to be of large size, and often have more complex sculpturing patterns.

Cucurbitales.—The Cucurbitaceae, considered derived from the Passifloraceae (Takhtajan, 1969), show more highly evolved pollen than the Passifloraceae (Jeffrey, 1964; Awasthi, 1962*a, b*; Saad, 1964; Marticorena, 1963). Pollen of several tribes in the subfamily Cucurbitoideae (Jeffrey, 1964) are similar to flacourtiaceous pollen. Pollen of the tribes Joliffieae, Melothrieae, Schizopeponeae and of the subfamily Zanonioideae are tricolporate, small, prolate, and finely reticulate. An equatorially elongate endoaperture is often present. More highly evolved types are found in the remaining tribes which include 4–10 apertures, pantoporate, and spinose grains. Clearly, pollen provides data compatible with the systematic position of the family.

Salicales.—Persistent suggestions have related the Salicaceae to the Flacourtiaceae, especially to Flacourtieae (Hutchinson, 1967) or Idesiinae (Gilg, 1925). Pollen of *Salix* is tricolporoidate or tricolporate with a reticulate sculpture and size (Risch, 1960) that is quite similar to that found in *Idesia* or *Itoa*. Pollen of *Populus* is inaperturate and derived. The data of Nair (1967) on pollen of Monochlamydeae, while not explicit on this relationship, is compatible with this scheme. Rowley and Erdtman (1967) have provided structural data by electron microscopy which will be of value for comparisons of similar studies of Idesiinae.

Begoniales.—The Begoniaceae and Datisceae produce pollen grains with some features similar to pollen of Flacourtiaceae. They are small, spheroidal to

perprolate and have an obscure sculpture. They differ in the presence of a striate pattern, having endoapertures with granulate membranes and occasionally being shed as tetrads. This group may be derived from Violales but is more distantly related.

Capparales.—Pollen of Capparaceae, while similar in some ways to the Flacourtiaceae, has evolved a thicker and more complicated reticulate exine with small spines.

Tamaricales.—The Tamaricaceae and Frankeniaceae have pollen which does not resemble that of the Flacourtiaceae. The grains are 2, 3, 4-colpate and may have granulate colpi membranes.

Malvales.—The Elaeocarpaceae have small, tricolporoid, prolate pollen quite similar to the Homalieae type within the Flacourtiaceae. With their finely reticulate pattern, these grains would not be readily distinguishable.

While pollen of the Tiliaceae is quite variable, that of the *Grewia* type is quite similar to flacourtiaceous pollen. It is not very different from the genus *Kiggelaria* (Chaudhuri & Mallik, 1965; Erdtman, 1952). Pollen of *Heritiera* is also quite similar to the Flacourtiaceae. The morphology of the compound apertures and of the exine is similar to that found in the Flacourtiaceae (Tarnavschi & Şerbănescu-Jitariu, 1968).

Pollen of the Sterculiaceae even more closely resembles that of the Flacourtiaceae. The tribe Sterculieae shows the closest pattern, especially the equatorially elongate endoapertures and the finely reticulate exine (Litchfield, 1966; Rao, 1950; Erdtman, 1964). (E.g. *Brachychiton* and *Argyrodendron* would fit easily among flacourtiaceous pollen.) Of the other tribes, pollen of the Buttnerieae is also not very different.

The tribe Prockieae, including the genera *Hasseltia* (Figs. 159–160), *Prockia* (Figs. 161–162), and *Neosprucia*, was removed from the Flacourtiaceae by Hutchinson (1959) and placed in the Tiliaceae. On the basis of pollen morphology, there is no support for the removal of these genera. They fit perfectly well among the Banarieae.

Among the Tiliaceae and Sterculiaceae are many genera showing highly evolved pollen including spininess, triangular shape, and elaborate porate apertures. Nevertheless, among the less specialized members of these families, a definite affinity can be found with the Flacourtiaceae. The pollen of these two families can be considered as a type distinct from malvaceous or bombacaceous pollen (Chaudhuri & Mallik, 1965).

Pollen grains of the Rhopalocarpaceae are medium to large, 3–6-colpate, colporate, and oblate. The exine is echinate or subechinate. In the past this group has been placed in the Violales (with the Cochlospermaceae), the Theales or Malvales, but recent studies by Huard (1965*a, b*) confirm their placement in the Malvales. They are not close to the Flacourtiaceae.

The Bombacaceae have pollen which are quite different from the Flacourtiaceae. Advanced trends include highly spinose, per-reticulate rugulate or verrucate exines, fossaperturate shape, or elaborate aperture patterns. (Tsukada, 1964; Fuchs, 1967; Robyns, 1963; Nair, 1962*b*).

Malvaceae have mostly large, spinose pollen with thick walls and large

apertures. Many are panporate. Pollen of this family has the least similarity to the Flacourtiaceae of all of the malvalian families (Prasad, 1963; Sharma & Rastogi, 1965; Bronckers & Horvat, 1963; Saad, 1960; Nair, 1962*b*; Chaudhuri & Mallik, 1965).

Euphorbiales.—The Euphorbiaceae have features in common with both primitive Violales and Malvales and may have arisen from an ancestral group between them (Takhtajan, 1969). Pollen of the subfamily Phyllanthoideae (Punt, 1967), especially that of the *Antidesma* and *Richeria* types (Punt, 1962), is quite similar to flacourtiaceous pollen. The grains tend to be prolate, costate, small- to medium-sized, have equatorially elongate apertures with diffuse ends, and are reticulate or psilate-tectate. Other genera are more specialized in being verrucate, per-reticulate, fossaperturate, spinose or suprabaculate, and have to 4–5 apertures. Some genera are stephanocolpate, -porate, or inaperturate. The subfamily Crotonoideae is considerably more specialized.

This large, diverse family may well have had its origins in the Violales. On the other hand, Chaudhuri and Mallik (1965) have pointed out an apparent affinity between the Sterculiaceae and Phyllanthoideae, because of resemblances in the tricolporate, spheroidal-oblate pollen of some genera.

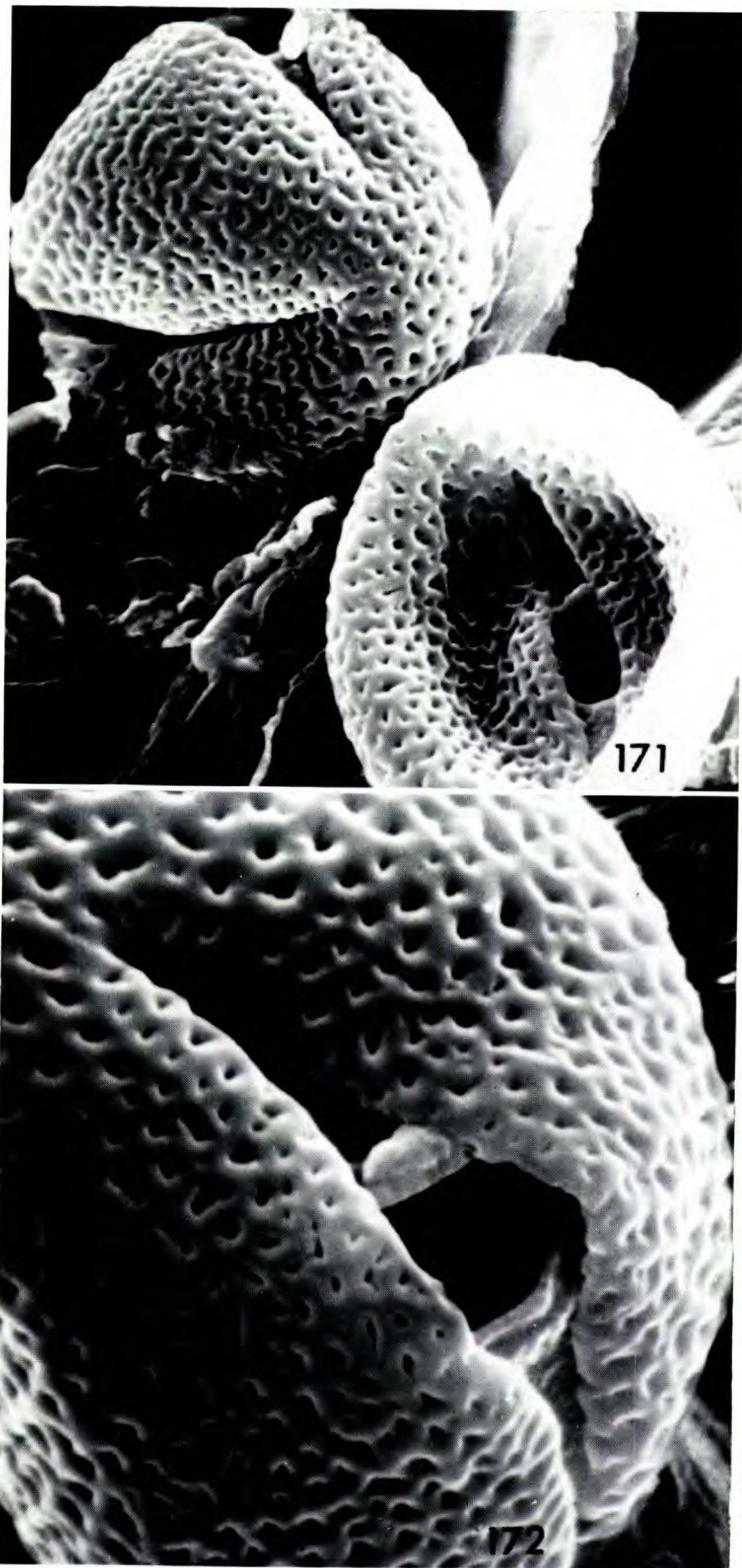
Dilleniales.—Studies by Dickison (1967), have shown the Dilleniaceae to have a variety of morphological types but, as with the Flacourtiaceae, the tribes cannot be delineated easily by pollen morphology. Dickison concluded that the Dilleniaceae show more resemblance to the Theales than to the Ranalian families. Violales were not considered closely related.

Direct comparisons in the present study show that the pollen of the Flacourtiaceae is quite compatible with that of the Dilleniaceae. Agreement includes the prolate to spheroidal shape, circular polar outline, small to medium size, tectate or semi-tectate structure, and finely reticulate to reticulate sculpture. Costae seem to be present but are not mentioned in Dickison's study. The compound apertures are somewhat different. The furrows are said to be provided with an operculum and often a margo. Trends toward four apertures and porate grains are paralleled in the Flacourtiaceae. It seems quite feasible to consider the Dilleniaceae a primitive connecting link between the Violales and Theales as stated by Takhtajan (1969).

Theales.—The Ochnaceae, a basal group in the Theales, have pollen which bears a strong resemblance to the Flacourtiaceae. The tricolporate, prolate, costate grains have an equatorially elongate endoaperture which is quite similar to the Flacourtiaceae. The ectexine is smooth, subverrucate, to finely reticulate (Muller, 1969). There is also an unmistakable resemblance to several higher families of Violales (Cochlospermaceae, Bixaceae, and Cistaceae).

Pollen of the Theaceae shows some similarities to flacourtiaceous pollen in size, shape, reticulate exine, equatorially elongate endoapertures, smooth colpi membranes, and costate margins. Some genera differ in having densely spaced pila, a spinuliferous ectexine, and granulate aperture membranes. The overall resemblance here is not as close as with the Ochnaceae.

The Clusiaceae (Guttiferae) and Hypericaceae have pollen with tendencies toward greater size, 4–5 apertures in an angulaperturate condition, and more



FIGURES 171–172. Pollen of Flacourtiaceae, tribe Casarieae, *Hecatostemon guazumii-folius* (Smith 174). Scanning electron photomicrographs of acetolyzed grains.—171. Oblique polar view and equatorial view of collapsed grain. $\times 2400$. Note reticulate surface.—172. View of aperture. $\times 5900$. Note equatorially elongate endoaperture disappearing from view beyond the edge of the colpus. An ectexine proliferation is visible extending along one side of endoaperture. It appears to originate on one side of the colpus margin. This ectexinal proliferation is also visible in both grains of Fig. 171.

highly specialized sculpture. A few species are tricolporate and finely reticulate. The equatorially elongate endoaperture is similar to the Flacourtiaceae.

Of the Theales, flacourtiaceous pollen most clearly resembles that of the Ochnaceae with the Theaceae, Clusiaceae, and Hypericaceae showing generally more highly evolved pollen.

It must be kept in mind that comparisons of the Flacourtiaceae with only the more highly evolved or "average" condition of other families could create a picture of the Flacourtiaceae as being a large isolated family. I have deliberately attempted to find genera and tribes which most resemble the Flacourtiaceae, thus pointing out possible phyletic bridges. This is a long way from demonstrating phylogeny, and I would hope that these suggestions might stimulate further investigation.

Comments on miscellaneous groups occasionally placed near the Flacourtiaceae.—The Canellaceae, at one time placed in the Parietales have been demonstrated (Wilson, 1964) to belong with the monosulcate Ranales closest to the Myristicaceae.

The Hoplestigmataceae have 6–9-angular, tricolporate, finely reticulate grains with a compound aperture not found in the above orders.

The Droseraceae have very specialized 7–8 porate, spinuliferous pollen. The family has possible affinities with the Centrospermae.

Sabouraea was described by Leandri (1962) and placed by him and by Hutchinson (1967) in the Flacourtiaceae. Its pollen, studied by Rethore (1963), is pantocolpate and altogether novel for the Flacourtiaceae. Its best home is still uncertain.

Barteria J. D. Hook., a myrmecophyte of west tropical Africa, has been treated as a member of the Flacourtiaceae (Wheeler, 1922). Pollen of *Barteria fistulosa* Masters is illustrated and described as being flacourtiaceous by Van Campo, Bronckers and Guinet (1965). Its pollen is spiny, polyporate, and has a diameter of about 165 μ . It is not flacourtiaceous; it has been included with the Passifloraceae by Spirlet (1965).

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